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SPATIAL PATTERNS OF THE WESTERN SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE) AND OPTIMAL SAMPLE SIZES FOR ESTIMATING POPULATION DENSITY OR CLASSIFYING EXPECTED DEFOLIATION IN THE PACIFIC NORTHWEST

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TABLE OF CONTENTS

Page

ABSTRACT

INTRODUCTION
- Spatial Pattern
  - Estimating Average Whole-Plot Density
- Sequential Count Plans
- Classifying Expected Defoliation

METHODS
- Budworm Trends
- Field Procedures
  - Supplemental Data
- Analytical Procedures
  - Spatial Pattern
  - Sequential Count Plans
  - Projecting Defoliation
  - Sequential Classification

SPATIAL PATTERN AND SEQUENTIAL COUNT PLANS
- Fourth Instars
  - Spatial Pattern
  - Standard Sampling
  - Sampling Short or Tall Trees
- Residual Pupae
  - Spatial Pattern
  - Standard Sampling
  - Sampling Short Trees
- Egg Masses
  - Spatial Pattern
  - Standard Sampling
  - Sampling Tall Trees

CLASSIFYING EXPECTED DEFOLIATION
- Projecting Defoliation
- Sequential Classification
  - Egg Masses
  - Fourth Instars

USING THE PLANS
General Considerations
Geographic Areas and Host Species
Precision
Budworm Density
Plot Size
Treatment Effects
Sequential Count Plans
Estimating Average Whole-Plot Density
Patterns of Budworm Occurrence
Area of a Sample Tip
Foliage Distribution
Classifying Expected Defoliation
Projecting Defoliation
Error Rates
Projecting Damage

IMPLICATIONS
Spatial Pattern
Sequential Count Plans
Estimating Average Whole-Plot Density
Classifying Expected Defoliation

SUMMARY

ACKNOWLEDGMENT

REFERENCES CITED

ABSTRACT

Between 1979 and 1982, sample units consisting of 45-cm terminal branch tips were drawn from host Douglas-fir and grand fir growing on sites in Washington, Idaho, Oregon, and Montana. Based on these sample units, spatial patterns of the western spruce budworm, Choristoneura occidentalis Freeman, were analyzed by Iwao's regression technique. Nominal fourth instars were not sampled on trees less than 7 m tall, and means and variances were usually about equal as mean densities approached the minimums sampled. Otherwise, budworm populations were more aggregated than random at all stages sampled [nominal fourth instars, residual pupae (pupae remaining after predation), and egg masses]; among all vertical crown strata [lower-, mid-, and upper-crown]; and on trees of all sizes [short (< 7 m), normally sampled (7 to 14 m), and tall (> 14 m)]. Analyses of tips drawn from the midcrown of normally sampled trees indicated that fourth instars are less aggregated than either residual pupae or egg masses. At each stage, a single insect (or egg mass) appeared to form the basic component of the population on 45-cm midcrown terminals.

Consistently, residual pupae were more aggregated on 45-cm branch tips drawn from the lower crown of normally sampled trees than among those drawn from the midcrown. The increased patchiness of the pupae on lower crown tips was attributed primarily to the activities of predaceous ants. The spatial pattern of residual pupae in the lower crown was also poorly described by the mean

crowding-mean density ($\overset{*}{m}$ - m) relation. Again, this poor correlation was ascribed primarily to patchiness in the species composition, distribution, and intensity of predation by colonies of ants.

Parameters from the mean crowding-mean density regressions were used to develop sequential count plans for all three budworm stages. For each stage, estimates of average density per square meter of foliage on normally sampled trees can be based on tips drawn from the midcrown of these trees. When estimates of fourth instar or pupal densities on short trees are needed, separate samples should be drawn from the midcrown of these trees. Similarly, separate fourth-instar or egg-mass samples should be drawn from the lower crown of tall trees, in places where estimates of these densities on tall trees are needed.

For budworm populations in the Pacific Northwest, recent data validate Carolin and Coulter's (1972) regression equation that uses fourth-instar density to project defoliation. In areas to the south or east, however, the equation projects much lower defoliation than was actually observed. As a way to classify expected defoliation in the Pacific Northwest, provisional sequential classification schemes were developed that use budworm densities on terminal tips of normally sampled trees. Separate schemes were developed for egg masses and fourth instars.

INTRODUCTION

In western North America, population densities of the western spruce budworm, Choristoneura occidentalis Freeman, are known to range over at least five orders of magnitude. Typically, populations are either at densities that are barely discernible by standard methods of foliage sampling, or at densities so high that defoliation is obvious. For example, a significant budworm outbreak has persisted in the northern Rocky Mountains since about 1948. For about 30 years before 1948, however, "...only scattered and insignificant infestations were reported..." (Fellin et al. 1983). Recent information on all aspects of the natural history of this pest is summarized in Brookes et al. (in press).

The central themes of this paper are to examine spatial patterns of the western spruce budworm and to describe optimal sample sizes for estimating budworm population density or classifying expected defoliation.

Spatial Pattern

Changes in the relative degree of aggregation (patchiness) of the western spruce budworm from nominal fourth instar to residual pupae (pupae remaining after predation) were closely associated with the mortality rate induced by birds and ants across this interval (Campbell et al. 1985). Both Iwao (1968) and Pielou (1969) show that relative aggregation is unchanged by mortalities that occur at random. Thus, during intervals when the spatial pattern of an organism is not changed by the inherent behavior of the population, changes in relative aggregation may provide insights about the action of mortality-causing

processes. Alternatively, when the inherent behavior of an organism results in a systematic shift in its degree of aggregation, that shift may provide insights about the evolution of the behavior pattern that induced the shift.

The objectives of the portions of this report that deal with spatial pattern are fourfold: to describe indices of spatial patterns of the western spruce budworm at the start of each of three life stages (fourth instars, residual pupae, and eggs); to compare these indices from one budworm stage to the next; to suggest some of the biological processes that may cause systematic differences in these patterns among vertical portions of the host trees; and to provide a basis for developing sampling schemes for the pest.

Sequential Count Plans

Estimates of western spruce budworm densities form the basis for most budworm-related field research; they are essential for making pest-management decisions and evaluating control tactics.

Optimal sampling methods provide these estimates with acceptable precision while minimizing costs. Experience by several investigators (Bechinski and Pedigo 1983, Kolodny-Hirsch 1986) suggests that sequential count plans approach this optimum. For that reason, the objectives of this portion of the study were to develop sequential count plans for western spruce budworm nominal fourth instars, residual pupae, and egg masses.

Estimating Average Whole-plot Density--Successive estimates of average budworm density per square meter of foliage across the whole plot provide the basis for most studies on budworm population dynamics. Factors that should be considered in using sequential count plans to derive these whole-plot estimates are described in the section titled, "Using the Plans."

Classifying Expected Defoliation

In pest management, classifying population density relative to a predetermined threshold that may trigger some management action is often important. Sequential classification is one method: several sequential classification plans have been developed, either for the spruce budworm, C. fumiferana (Clem.) or C. occidentalis (Morris 1954, Waters 1955, Cole 1960, McKnight et al. 1970).

The objectives of this phase of the study were to develop two sequential classification schemes for the western spruce budworm. One scheme provides a way to classify expected defoliation at the end of a season from egg-mass densities found during the preceding fall on midcrown 45-cm terminal branch tips of normally sampled trees. The second scheme provides a way to classify expected defoliation from densities of nominal fourth instars found during that season on midcrown terminals.

METHODS

As part of 1979-82 studies on the population dynamics of the western spruce budworm, terminal 45-cm branch tips were removed from host Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco, and grand fir, Abies grandis (Dougl. ex D. Don) Lindl., growing on sites in Washington (four sites), Idaho (four sites), Oregon (nine sites), and Montana (nine sites). In every site studied, the foliage on these two species represented over 90 percent of the total foliage for this insect. The sites and stands used in each state are described in Campbell et al. (1984a).

Budworm Trends

In eastern Oregon, two of the nine sites were established in stands with no recent history of defoliation, and at a time when budworm densities were low. During the study, these populations increased. In the seven remaining sites, the budworm populations had already caused noticeable defoliation at the time studies were initiated. In retrospect, the Oregon budworm populations were clearly studied during an early phase of a major outbreak.

Budworm populations were studied on four stands in central Idaho. At the time of the study, defoliation of three of the stands was light to moderate. The fourth stand had only a trace of defoliation. During the study years, populations on all four of these sites remained fairly stable. Two areas were studied in Montana--one in the northwest and the other in the southwest. In northwest Montana, budworm populations were moderately dense on two sites and

sparse on a third. During the study, the populations increased on all three sites. In southwest Montana, all six of the stands had already experienced defoliation for at least 6 years.

Four sites were studied in north-central Washington. Defoliation on these sites was noticeable in 1979, the first year of the study. By 1981, the budworm populations on all four sites had collapsed.

In summary, the nine budworm populations studied in Oregon represented an early phase of a major outbreak; the 13 populations in Idaho and Montana were part of dynamically stable, low-intensity outbreaks; and the four populations in Washington were studied during a period of outbreak decline.

Field Procedures

Sampling was done three times during each budworm generation: first, when most of the insects were in fourth instar; second, when adult emergence was about 95 percent complete; and third, when egg mass deposition was complete. For all routine sampling, branch tips were removed by two-person crews using pole pruners. To obtain samples from tall trees (>14 m tall), a truck-mounted, 90-foot hydraulic lift was used for sampling nominal fourth instars and residual pupae. Tree climbers obtained samples from tall trees examined for egg masses.

Foliage in the first sample was examined for new buds and larvae in field laboratories. Beginning in 1981, the method of Martineau and Benoit (1973) was

used to facilitate these examinations. Foliage from the second sample was examined for dead pupae and pupal exuviae in the field. Foliage from the third sample was examined for new egg masses in field laboratories, by the method of Buffam and Carolin (1966). These third samples were also examined for defoliation of current-year growth.

For each of the three budworm stages sampled, the states used, years of use, number of sites from which samples were drawn, range in the number of samples drawn per site, and range in the mean number of insects found per sample are shown in Tables 1-3.

Supplemental Data--Two further data sets used in this study were accumulated by Forest Pest Management personnel in the USDA Forest Service. The first of these data sets was collected from an area near Butte, in southwestern Montana. These data are a portion of the information gathered in a pilot control project against the western spruce budworm with Bacillus thuringiensis Berliner (B.t.). The material was applied during 1981. The second set was collected from an area in northern New Mexico. These data were gathered to evaluate a suppression project against the budworm using carbaryl, which was applied in 1977. Similar methods were used in both areas to estimate budworm density and defoliation (Parker et al. 1978, 1979; Parker and Ragenovich 1980; Ragenovich and Parker 1981; and Stipe et al. 1983).

In this paper, these supplemental data were used to evaluate relations between densities of nominal fourth instars and subsequent defoliation.

Analytical Procedures

Spatial Pattern--To estimate the spatial pattern of the budworm populations, Lloyd's (1967) mean crowding index ($\overset{*}{m}$) was calculated for each budworm stage, site, and year. For whatever sampling unit is used, mean crowding is defined as the mean number of other individuals per individual per unit, and is calculated as $\overset{*}{m} = m + [\sigma^2/m - 1]$. Here, m is mean budworm density per 45-cm terminal tip and σ^2 is the variance in m. For each budworm stage, mean crowding of the populations studied was linearly regressed on mean density as $\overset{*}{m} = \alpha + \beta m$ (Iwao 1968), to obtain least-squares estimates of α and β. Subsequently, for each budworm stage, the relation between the mean and the variance was estimated according to the formula $\sigma^2 = (\alpha + 1)m + (\beta - 1)m^2$ (Iwao and Kuno 1968).

The parameters α and β are biologically relevant descriptors of aggregation. The parameter α describes the size of the basic component of the population on the sample unit, and β describes the spatial pattern of this component. If $\alpha = 0$, then the basic component of the population ($\alpha + 1$) is an individual insect (or egg mass); if $\alpha = 1$, then the basic component of the population is two insects or egg masses, and so on. If β is less than 1, equal to 1, or greater than 1, then the distribution of the basic components is respectively more regular than random, random, or more aggregated than random.

Sequential Count Plans--For each of the three insect stages, sequential count plans were calculated by Kuno's (1969) formula:

$$T_n = (\alpha + 1) / [D_o^2 - (\beta - 1)/n];$$

Where T_n is the cumulative density of insects (or egg masses) found on 45-cm terminal tips; D_o is the ratio of the standard error of the mean to the mean (a fixed precision); α and β are estimates of coefficients from Iwao's regression; and n is the number of 45-cm sample units.

Projecting Defoliation--A model descibed by Carolin and Coulter (1972) was used to evaluate relations between fourth instars per 100 buds and percent defoliation. With the use of indexing variables and standard regression procedures (Neter and Wasserman, 1974) the model was simultaneously tested against three data sets: from the Pacific Northwest between 1979 and 1981 (n = 14); from an area in southwestern Montana (n = 9); and from an area in northern New Mexico (n = 48).

Sequential Classification--The sequential classification schemes for fourth instars and egg masses are based on the following critical densities (m_o), as adapted from Carolin and Coulter (1972):

Egg masses per 45-cm tip	Larvae per 45-cm tip	Expected defoliation
< 0.4	< 3	Light
0.4 - 1.0	3-8	Moderate
> 1.0	> 8	Heavy

Acceptance and rejection lines were calculated for each of the above critical densities, using methods described by Iwao (1975) as

$$T_n = nm_o \pm 1.96 \sqrt{n[(\alpha + 1)m_o + (\beta - 1)m_o^2]},$$

Where T_n is the cumulative number of insects at the upper (+) or lower (-) limit of the decision lines, n is the number of 45-cm branch tips, m_o is the

critical population density per tip, and 1.96 is the t-value for a 95-percent confidence limit.

Although only Iwao's (1975) procedure is developed in this paper, Wald's (1947) sequential probability ratio test could also have been employed, using the relation $k = 1/(\beta-1)$ to estimate the common k, and the negative binomial plan described by Wald.

At any given time and place, the spatial pattern of a population reflects both the inherent behavior of that population and physical and biotic attributes of the environment. For these reasons, a brief review of the relevant natural history of the western spruce budworm as specific results are presented seems appropriate.

Fourth Instars

In the Pacific Northwest, budworm emergence from the egg masses is usually completed by late August, when the first of two major larval dispersal episodes occurs. Many of the newly hatched larvae drop from the foliage on silken threads and may be dispersed by the wind. Ultimately, the larvae settle down and spin hibernaculae, often under bark scales and lichens. On Douglas-fir, many of these hibernation sites are on the trunks of the trees (Terrell 1959).

The second major dispersal period commences early in May of the following year, when the second instars emerge from hibernation. Once again, many of the larvae drop on threads and are dispersed by the wind. Variation in budworm survival induced during the two larval-dispersal episodes is a major contributor to year-to-year variation in budworm density (Thomson et al. 1984, Campbell in press). In interior western forests, silvicultural recommendations for budworm-susceptible stands are based partly on relations between the amount and placement of host foliage and the dispersal requirements of the larvae (Carlson et al. 1983, Schmidt et al. 1983).

Survivors from the second dispersal episode mine into either needles or buds on host trees. Third instars leave the mined needles and buds and begin feeding on the newly opened vegetative shoots by late May or early June. In the Pacific Northwest, the bulk of the population passes through fourth instar from about mid-June to early July, depending largely on latitude, longitude, elevation, and aspect. By this time, the new shoots are fully expanded.

Spatial Pattern--Mean densities of nominal fourth instars among the 31 data sets drawn from the midcrowns of normally sampled trees ranged from 0.018 to 17.633 larvae per midcrown 45-cm branch tip (Table 1). Among these 31 mean densities, six were less than one larva per tip and six were greater than ten.

Regression of mean crowding ($\overset{*}{m}$) as a function of mean density (m) (fig. 1) yielded

$$\overset{*}{m} = 0.688 + 1.369\ m, \ (R^2 = 89.7\%).$$

Standard deviations for the intercept (α) and the slope (β) were $\pm$ 0.646 and $\pm$ 0.085, respectively. The intercept value (α) was not significantly greater than zero, which suggests that an individual larva forms the basic component of the population on 45-cm midcrown terminal branch tips. Nevertheless, for two reasons, the intercept was retained. First, retention of this parameter yields more conservative sampling plans. Second, in a sampling study on larval populations of C. fumiferana) in Ontario, Regniere and Sanders (1983) also regressed mean crowding on mean density per 45-cm midcrown branch tip. Their regression, which was based on 103 data sets, yielded

$$\overset{*}{m} = 0.715 + 1.16\ m,$$

and their intercept was significantly different from zero ($P < 0.01$). Additional observations on western spruce budworm populations should resolve questions about the reality or non-reality of a non-zero intercept for fourth instar western spruce budworm larvae on 45-cm midcrown tips.

For western spruce budworm larvae, the slope ($\beta = 1.369$), which is significantly greater than 1 ($P < 0.01$), suggests that the larvae have an aggregated distribution. Their common k value (2.71), where $k = 1/[\beta - 1]$, also indicates a rather strongly aggregated larval population.

In contrast to the above, Cole (1960) derived a common k of 7.736 for western spruce budworm larvae on 15-in (37.8-cm) branch tips drawn from about 60-ft-(18.3-m)-tall Douglas-fir in the northern Rocky Mountains. For C. fumiferana in northeastern states, Waters (1955) derived a common k of 7.228 for larval populations on 15-in branch tips. For C. fumiferana in Ontario, the results presented by Regniere and Saunders (1983) would yield $k = 6.25$ for larvae on 45-cm tips. Collectively, these results suggest that late instar populations of the western spruce budworm in the Pacific Northwest may be somewhat more aggregated than their counterparts to the east.

Standard Sampling--Sample sizes required to achieve various precisions relative to the mean for nominal fourth instars on midcrown tips of normally sampled trees are shown in Table 4 and fig. 2. In this and following tables, critical stop points for each specified precision are described in terms of both the cumulative minimum number of insects that must be found on a given number of

sample tips (Table 4A), and the cumulative minimum number of sample tips required for a given average density per tip (Table 4B).

The number of 45-cm sample tips required to achieve 20-percent precision relative to the mean are shown for various means in Table 5 for both C. occidentalis on Douglas-fir and grand fir in the northwestern United States and C. fumiferana on balsam fir, A. balsamea L., and white spruce, Picea glauca Moench. (Voss), in northwestern Ontario. Regniere and Sanders (1983), in the cited sampling paper for larvae of C. fumiferana, ultimately chose Taylor's power law (Taylor 1961) in preference to Kuno's (1969) method to relate C. fumiferana larval means and variances. Nevertheless, the optimal sample sizes specified for the two pests are remarkably close.

Earlier, Srivastava et al. (1984) specified that a precision of 20 percent could be obtained for nominal fourth instars of C. occidentalis on normally sampled trees by sampling one 45-cm tip from each of 15 trees, at a density of 100 nominal fourth instars per square meter of foliage on terminal tips. An average of 0.082 $\pm$ 0.012 square meters of foliage per tip was found among the several thousand 45-cm terminal branch tips that were drawn between 1979 and 1982 in the Pacific Northwest. Thus, 100 fourth instars per square meter of tip foliage represents about 8.2 fourth instars per tip. As expected, the number of tips specified in Table 4 to attain a precision of $\pm$ 20 percent at an everage density of 8.2 larvae per tip, is very close to the 15 tips that were specifiec in the paper just cited.

Sampling Short or Tall Trees--Limited data suggest that fourth instar densities may be somewhat higher on tall trees (> 14-m) than on normally-sampled ones (Campbell et al. 1983a). While those data are very sparse, they suggest that fourth instar densities on terminal tips drawn from the lower crown of those tall trees could be used to represent fourth instar densities on the whole tree.

Unfortunately, short (< 7-m tall) trees were not sampled for nominal fourth instars. In places where such trees represent a significant portion of the total, and where high precision is needed, a separate larval sample should be drawn from these short trees.

In the absence of adequate empirical data on fourth-instar spatial pattern on tips of short or tall trees, the sampling plan developed for this stage on midcrown tips of normally sampled trees (Table 4) is the best available guide to estimate optimal sample size for trees in each of the three height classes.

Residual Pupae

Until about the fourth instar, the larvae spend most of their time inside a mined needle or an expanding shoot. During the next 3 to 4 weeks, the growing larvae spin silken feeding tubes among the needles of the current year. Many of the insects pupate in these tubes, although a substantial fraction move back from the new shoots and pupate on older foliage. The mature larvae always spin a network of threads, which surround and cradle the pupae.

Western spruce budworm larvae and pupae are especially vulnerable to predation in the interval between fourth instar and adult emergence. Budworm survival was consistently only about 5 percent across this interval, in populations where fourth instar density was less than one larva per square meter of foliage. After a series of exclosure trials in north-central Washington, eastern Oregon, central Idaho, and northwestern Montana, Campbell (in press) reported that average survival across this interval increased to about 40 percent on trees where predaceous birds and ants were excluded. Campbell concluded that predation by birds and ants can maintain most budworm populations in the Pacific Northwest at sparse densities indefinitely, unless other processes (such as unusually high survival during larval dispersal or aggregation of egg masses by the adult female moths) upset low density stability.

Spatial Pattern--On normally-sampled trees, mean densities of residual pupae (Table 2) ranged from 0.007 to 3.846 per midcrown 45-cm branch tip (n = 39), and from 0.027 to 2.409 per lower crown 4-m tip (n = 35). On short (4- to 7-m tall) trees, mean pupal densities ranged from 0.167 to 2.033 per midcrown tip among the eight data sets that were drawn.

In 28 data sets, non-zero mean densities of residual pupae were observed on both midcrown and lower crown tips of normally sampled trees. For each of these data sets, both the two means and estimated values of their negative binomial parameter k are shown in Table 6. Here, k is approximated as follows:

$$k = m^2/(s^2 - m).$$

According to values of k, pupae on lower crown tips were more aggregated than those on midcrown tips in 22 of the 28 data sets. Pupae on midcrown tips were more aggregated than those in the lower crown in only 5 of the 28 sets. In one set, aggregation was the same in both crown strata. A chi-square test (x^2 = 10.75 on 1 d.f.) shows that the degree of aggregation of residual budworm pupae is very unlikely (P ≐ 0.001) to be the same between these two crown strata.

Recently, Campbell et al. (1985) showed that predation on the western spruce budworm by birds and ants was closely correlated with increases in budworm aggregation across the interval from fourth instar to residual pupae. We inferred that these predator groups not only tend to concentrate more effort on some trees than on others, but also continue to concentrate on the favored trees even after prey densities on these trees have been reduced below the average density for a larger spatial unit. Further, results described in Campbell and Torgersen (1983) and Campbell et al. (1984b) strongly suggest that ants play their most important role as budworm predators among budworm cohorts that are relatively close to the ground.

From the results presented in Table 6 and the information just cited, I infer that predaceous ants were probably primarily responsible for the increased patchiness of budworm pupae on lower crown tips.

Regression of mean crowding (m) as a function of mean density on midcrown tips of normally sampled trees (fig. 3) yielded

$$m = 0.033 + 1.571\ m, \qquad (R^2 = 87.0\%).$$

Standard deviations for the intercept (α) and the slope (β) were $\pm$ 0.138 and $\pm$ 0.098, respectively. Clearly, the intercept value for residual pupae on midcrown tips did not differ significantly from zero. Thus, an individual insect forms the basic component of the pupal population on midcrown 45-cm tips, and the equation for $\overset{*}{m}$ reduces to $\overset{*}{m} = 1.571m$. The slope ($\beta = 1.571 \pm 0.098$), which is significantly greater than 1 ($P < 0.01$), suggests that residual pupae on midcrown tips are somewhat more aggregated than the preceding fourth instars (recall that $\beta = 1.369 \pm 0.085$ for fourth instars).

In comparison, regression of mean crowding as a function of mean density on lower crown tips of normally sampled trees (fig. 4) yielded

$$\overset{*}{m} = 0.474 + 1.646\ m, \qquad (R^2 = 66.6\%).$$

Standard deviations for α and β in this crown stratum were $\pm$ 0.216 and $\pm$ 0.199, respectively. Thus, the intercept (α) was significantly greater than zero ($P < 0.01$), and the slope (β) was significantly greater than one ($P < 0.01$).

On the one hand, the values of the above slope and intercept emphasize the patchiness of residual budworm pupae on lower crown tips. On the other hand, the relation between $\overset{*}{m}$ and m in this stratum is relatively poor ($R^2 = 66.6\%$), despite the obvious autocorrelation between the two variables. In particular, the wide scatter of points around the slope β, is compatible with the patchy occurrence of ants observed preying on pupae (Youngs and Campbell 1984). I believe the wide scatter of points in this figure reflects underlying patchiness in both the species composition and distribution of colonies of

predaceous ants, as well as variation in the intensity of ant predation on the budworm during the time interval across which the prey insects are pupating.

Clearly, the reliability of both Kuno's (1969) and Iwao's (1975) formulas depends on the reliability of the estimates of α and β derived from the m^* - m relation. Thus, the poor correlation between m^* and m derived for residual pupae on lower crown tips should be interpreted as a caution against selecting the lower crown as the preferred stratum for sampling. Further, because of the greater clumpiness of pupae in the lower crown, a considerable savings in sample size can be achieved by sampling midcrown rather than lower crown tips to estimate density at this stage.

For residual pupae on midcrown tips of short trees (4 to 7 m tall), regression of mean crowding on mean density (fig. 5) yielded $m^* = -0.198 + 1.805\ m$, (R^2=95.7%). For this stratum, standard deviations for the intercept and slope were $\pm$ 0.191 and $\pm$ 0.144, respectively. These values suggest that an individual pupa forms the basic component of the population in this stratum, so the equation reduces to $m^* = 1.805\ m$. Both the relatively steep slope of this equation and the common k (k = 1.24), for these points suggest that budworm pupae exhibit a particularly patchy distribution on short trees.

Standard Sampling--Sample sizes required to achieve various precisions relative to the mean for residual pupae on midcrown terminal tips of normally sampled trees are shown in table 7 and fig. 6.

Srivastava et al. (1984) estimated that a precision of 20 percent could be obtained for estimates of residual pupae by sampling one 45-cm terminal tip from the lower crown of each of nine normally sampled trees, at a density of 40 residual pupae per square meter of foliage on lower crown terminals, or about 3.3 pupae per tip. Surprisingly, that sample size is less than half the size that would have been specified if a sampling scheme had been developed for pupae in the lower crown from the $\overset{*}{m}$ - m relation found on lower crown tips of normally sampled trees. In the paper just cited, the investigators were able to account for only 69 percent of the among-tree variance in the density of residual pupae on lower crown tips, which was described as a second-degree polynomial function of the sample means. The discrepancy between the two estimates of the lower crown sample size needed to achieve a specified precision emphasizes my previously expressed concern that the rather unpredictable patchiness of residual pupae in the lower crown makes this crown segment a poor candidate for sampling.

Sampling Short Trees--Campbell et al. (1984a) reported that average pupal densities on tall trees were a close linear function of pupal densities on normally sampled trees. Unfortunately, however, pupal densities on short trees were not closely related to those on normally sampled ones. In places where trees less than 7 m tall make up a substantial portion of the stand, densities of residual pupae on these trees should be estimated through a separate subsample drawn from the midcrowns. Sample sizes required to achieve various precisions relative to the mean on midcrown tips of tree 4 to 7 m tall are shown in table 8 and fig. 7.

Egg Masses

On emergence from their pupal cases, adult female western spruce budworms deposit several egg masses--each mass usually consisting of about 40 to 50 eggs. Typically, they lay their first mass near their place of emergence. Subsequent egg masses may be laid many kilometers away by the strong-flying adults. Thus, deposition patterns among egg masses are related to both the location of the pupal case from which the adult moths emerged and behavioral responses by the females to a complex of environmental variables. Campbell et al. (1984a) invariably found higher egg-mass densities in the tops of host trees. In all-aged stands, the highest egg-mass densities have also invariably been found on tall trees.

At least in small (5-ha) plots, observed budworm egg densities were sometimes greater than the ability of resident females to produce eggs (Campbell et al. 1983b). Apparently, patterns of adult female behavior that result in redistributions of egg mases can profoundly influence the population dynamics of this pest.

Spatial Pattern--Mean densities of egg masses (Table 3) ranged from 0.028 to 4.25 per midcrown 45-cm branch tip drawn from normally sampled trees (n = 36), and from 0.056 to 3.111 per lower crown 45-cm branch tip drawn from tall trees (n = 13).

Regression of mean crowding ($\overset{*}{m}$) as a function of mean egg-mass density on midcrown tips of normally sampled trees (fig. 8) yielded

$$\overset{*}{m} = 0.271 + 1.666\ m, \quad (R^2 = 86.0\%).$$

Standard deviations for the intercept and the slope were $\pm$ 0.154 and $\pm$ 0.113, respectively. Here, the intercept value was only different from zero at P $\doteq$ 0.1, which suggests that an individual egg mass forms the basic component of the budworm population on 45-cm midcrown tips. As before, however, the intercept was retained, to help ensure that sampling plans for this stage would be conservative. The slope for egg masses on normally sampled trees is significantly greater than one ($P < 0.01$). Comparison between this slope (β = 1.666 $\pm$ 0.113) and those derived from this same crown stratum and tree height class for nominal fourth instars (β = 1.369 $\pm$ 0.085) and residual pupae (β = 1.571 $\pm$ 0.144), suggests that egg masses are more aggregated than fourth instars and at least as clumped as residual pupae, at least on midcrown terminals.

Regression of mean crowding as a function of mean egg mass density on lower crown tips of tall trees (fig. 9) yielded

$$\overset{*}{m} = 0.422 + 1.327\ m, \quad (R^2 = 73.6\%).$$

In this crown stratum, standard deviations for the intercept and slope were $\pm$ 0.292 and $\pm$ 0.226, respectively. Although the intercept was only significantly different from zero at about P = 0.2, it was retained to help ensure conservative sampling plans for this stratum. Like all the preceding regressions relating $\overset{*}{m}$ and m, this slope was significantly greater than one ($P < 0.01$).

The egg mass populations studied in the Pacific Northwest yield common k values of 1.50 on midcrown tips from normally sampled trees, and 3.06 for lower crown

tips from tall trees. For comparison, McKnight et al. (1970) derived a common k of 5.106 for egg masses on 24-in (60.96-cm) branch tips drawn from 50-to 70-ft-(15.3-to 20.3-m)-tall Douglas-fir in southern Colorado. For egg masses of C. fumiferana in New Brunswick, Morris (1954) derived a common k of 2.019 on whole branches drawn from the midcrown of trees where the midcrown could be reached by crews with pole pruners. For "very tall" trees, Morris derived a common k of 5.232 for egg masses on branches chosen to represent the whole tree. Comparison among these three sets of results suggests that egg masses of both these budworm species may be somewhat less aggregated on the tallest host trees.

Standard Sampling--Sample sizes required to achieve various precisions relative to the mean for egg masses are shown for midcrown tips of normally sampled trees in Table 9 and fig. 10.

Srivastava et al. (1984) estimated that a precision of 20 percent could be obtained for egg masses by sampling one 45-cm midcrown tip from each of 48 normally sampled trees at a density of 10 egg masses per square meter of foliage on midcrown tips, or about 0.82 egg masses per tip. As expected, this value is close to the number of tips specified for this budworm stage by the scheme presented here (Table 9).

Sampling Tall Trees--In general, average egg-mass density on both short and tall trees is a close linear function of average density on normally sampled ones. Where densities on normally sampled trees were less than about 2 egg

masses per square meter, however, densities on tall trees ranged from near zero to about 22 egg masses per square meter (Campbell et al. 1984a). Clearly, low egg-mass densities on normally-sampled trees could be misleading in stands that contain a significant number of tall trees.

Although the relation between $\hat{m}$ and m on lower crown tips of tall trees is relatively poor (R^2 = 73.6%), the egg-mass sampling plan for this stratum (Table 10, fig. 11) does provide a means for estimating density on this hard-to-reach foliage.

Projecting Defoliation

Projected defoliation of current-year growth is commonly used by pest managers to indicate expected damage to the stand. Specifically, for example, sequential classification schemes can be particularly useful where categorizing pest density in terms of expected defoliation is sufficient. Clearly, the utility of such schemes depends in part on a satisfactory ability to project expected defoliation as a function of current pest density. Predictive equations for relating western spruce budworm density to expected defoliation have been developed by several investigators (Carolin and Coulter 1972, 1975; Bullard and Young 1980). Also, Johnson and Denton (1975) describe several unpublished predictive equations on this same topic that had been developed for the northern Rocky Mountains by Terrell and Fellin.

To predict defoliation by the western spruce budworm, Tunnock[1] used egg-mass samples drawn from each of three major forest types: Douglas-fir east of the Continental Divide in Montana; Douglas-fir west of the Continental Divide in Montana; and mixed grand fir/Douglas-fir type in northern Idaho.

[1] Tunnock, S. Western spruce budworm egg masses for predicting defoliation potential in the northern region. USDA For. Serv./Northern Region. Rept. 74-27. 10 p. 1974.

In each forest type, Tunnock found poor correlations between eggs per 100 buds and subsequent defoliation, but his analyses also showed that these relations differed among the three forest types. Tunnock concluded that: "A regression line based on western Montata data could not be used to predict what would occur in eastern Montana." From any given egg density, Tunnock's regressions project much higher defoliation on Douglas-fir east of the Continental Divide.

Bullard and Young (1980) developed a series of equations that use egg-mass density to predict defoliation caused by the western spruce budworm on Douglas-fir. These equations are based on westwide data collected from 1976 to 1979. They found that a linear model between defoliation and egg-mass density explained less than 50 percent of the variation in defoliation, and that factors such as slope, aspect, and elevation may modify this relation considerably. Carolin and Coulter (1972), however, found a close relation between egg-mass density and subsequent defoliation in eastern Oregon.

Unfortunately, recent data do not provide much support for the relation between egg-mass density and subsequent defoliation described by Carolin and Coulter. Defoliation that would have been predicted from preceding egg-mass density by Carolin and Coulter (1972) tended to be higher than observed defoliation among the collapsing budworm populations in north-central Washington, and lower than observed defoliation among the populations representing the expanding outbreak in eastern Oregon.

Until further information is available on sources of variability in the relation between egg-mass density and subsequent defoliation, predicting

defoliation from density during some subsequent budworm stage would be prudent--or at least provisional projections based on egg masses should be checked with density estimated during a subsequent stage, before a final treatment decision is reached.

A linear model from Carolin and Coulter (1972) describes percent defoliation (Defol) of current-year growth as the following function of larvae (nominal fourth instars) per 100 buds on 45-cm branch tips (N_L):

$$\text{Defol} = 2.44 + 1.67\ N_L$$

This model yielded a remarkably close relation between these variables (R^2 = 95%) for the data set used by Carolin and Coulter (1972).

The above model was also significant for relating fourth-instar density per 100 buds on 45-cm sample tips to current-year defoliation in data sets drawn from three areas: the Pacific Northwest, southwest Montana--but east of the Continental Divide, and northern New Mexico. Using these three data sets, the following models were developed:

$\text{Defol} = 3.0 + 1.60\ N_L$; if Pacific Northwest, (n = 14);

$\text{Defol} = 3.0 + 4.09\ N_L$; if southwest Montana, (n = 9);

$\text{Defol} = 3.0 + 2.61\ N_L$; if northern New Mexico, (n = 48).

For the combined data set (n = 71), R^2 = 87%.

For each of the three areas, the data points and the least-squares regression line derived from the appropriate equation are shown in figs. 12-14. These

findings are summarized in fig. 15, together with results of prior research on this topic conducted in eastern Oregon by Carolin and Coulter (1972, 1975).

Like the results described by Tunnock, [1] the above results project much higher defoliation from any given larval density in stands east of the Continental Divide. Also, as summarized in fig. 15, when Carolin and Coulter (1975) compared relations between larval density and defoliation on Douglas-fir and grand fir, they found higher defoliation on grand fir. In more recent data, however, significant differences could not be detected in this attribute between the two hosts in the Pacific Northwest.

Differences in defoliation among regions and between host species could result from differences in any or all of the following: bud size or foliage produced per bud; synchrony between the budworm and its hosts; mean budworm weight at pupation; or mortality rates from fourth instar to pupation. Based largely on unpublished data, I suspect that one principal reason for the regional differences summarized in fig. 15 is systematically lower budworm survival from fourth instar to pupation in the Pacific Northwest, as compared to populations to the south or east.

These results strongly suggest that Carolin and Coulter's (1972) regression equation provides an accurate way to project defoliation in the Pacific Northwest as a function of preceding fourth-instar density.

Sequential Classification

Egg Masses--Two provisional sequential plans suitable for classifying egg mass density on 45-cm midcrown tips of normally sampled trees in terms of expected defoliation at the end of the following season are shown in Table 11. In Table 11A, expected defoliation is classified as light in situations that are classified as having less than 0.4 egg masses per tip. Moderate-to-heavy defoliation is projected when average density is classified as more than 0.4 egg masses. Similarly, in Table 11B expected defoliation is classified as light-to-moderate where average density is classified as less than 1.0 egg masses per tip, and heavy where average density is classified as more than 1.0 egg mass per tip. This same information is summarized graphically in fig. 16.

Fourth Instars--Two sequential sampling plans suitable for classifying nominal fourth-instar density in terms of expected defoliation at the end of the current season are shown in Table 12 and fig. 17. In Table 12A, expected defoliation is classified as light when populations average less than three fourth instars per 45-cm tip. Moderate-to-heavy defoliation is expected when average density is classified as more than three insects per tip. Similarly, in Table 12B, expected defoliation is classified as light-to-moderate where average density is classified as less than than eight insects per tip, and heavy where average density is classified as more than eight insects per tip.

USING THE PLANS

General Considerations

Collectively, the usefulness of the plans presented here depends on the stability of three biological patterns. First, the ability of each count plan to specify optimal sample size accurately depends on a reliable spatial pattern at each budworm stage (fourth instars, residual pupae, and egg masses) on 45-cm branch tips. Second, the accurate estimation of average whole-plot densities from densities on sample tips depends on intrastand patterns of budworm occurrence that are consistent with those described in Campbell et al. (1984a). Third, the ability to classify expected defoliation accurately depends on a reliable relation between egg-mass or fourth-instar densities per 100 buds and subsequent defoliation.

Geographic Areas and Host Species--Differences in spatial patterns of the budworm on sample tips, among geographic areas and between host species were not sufficient to justify the development of separate count plans by either area or host species for any of the three budworm stages. Naturally, however, each of these plans should be validated before any are used on a broad operational scale.

Differences among geographic areas and between host species must be considered in both estimating average whole-plot densities and classifying expected defoliation. These considerations are described in subsequent sections of this paper.

Precision--Optimal sample size varies inversely with population density. Consequently, precise estimates become increasingly expensive to obtain as density decreases. Further, each of the sequential count plans presented here used a 65-percent confidence interval to estimate optimal sample sizes. Where more than 65 percent of the estimates must fall within the interval, more samples would have to be taken. For example, if a 95-percent confidence interval is specified for a study on budworm population dynamics, optimal sample size would increase almost fourfold for every given budworm density and precision.

Clearly, in any given study, the precision that is acceptable should be defined by the intended uses of the sample data. Nevertheless, as noted by Southwood (1978): ". . . the law of diminishing returns applies as one attempts to reduce the statistical errors of sampling and, in the long run, more knowledge of the ecology of the animal may be gained by studying other areas or making other estimates or even by just taking further samples than by straining for a very high level of accuracy in each operation." For damage assessment and control studies on numerically volatile insect pests, Southwood suggests: "... an estimate of population density with a standard error of aboout 25% of the mean ... ." For life-table studies, he notes that "... the level is frequently set at 10%."

Budworm Density--Among the data sets used to develop the sampling schemes presented here, maximum mean densities were about 17 fourth instars, 4 residual pupae, or 4 egg masses per 45-cm midcrown tip drawn from normally sampled trees. As mean budworm densities rise above these observed values, differences

in density among sample tips probably tend to decline. Thus, the equations presented here would probably yield conservative estimates of sample sizes required to reach any given precision among more dense populations. Because optimal sample size varies inversely with population density, conservative estimates at high densities should not represent a problem in applying any of the count plans.

Minimum mean densities were about 0.1 insect (or egg mass) per tip among the populations used to develop the sampling schemes presented. Means and variances were usually about equal among these least dense populations, but each of the equations developed to describe spatial patterns on sample tips is based on values of β that project a clumped pattern of budworm occurrence at all densities. Thus, each equation would probably seriously overestimate required sample sizes to achieve any specified precision where densities are below those used to develop these equations. To estimate sample size where population densities are below about 0.1 larva, pupa, or egg mass per tip, the cumulative number of insects (or egg masses) that must be counted ($T_{n)}$ to reach a fixed precision (D_o) can be estimated as $T_n = 1/D_o^2$.

Plot Size--To use any of the plans presented here, it is crucial that the sampling distributions must not differ systematically from those on which the plans are based. Specifically, because the samples used to develop these plans were drawn from 5-ha blocks, the plans cannot be expected to provide satisfactory precision unless the samples used to calculate each sample mean are all drawn from a similar spatial unit. To use any of these plans in larger forested units, samples should be obtained from a series of representative

subunits. Naturally, enough subunits should be established to assure that they collectively represent the larger area.

Treatment Effects--To my knowledge, evidence is lacking on the effect of pesticides on post-treatment intrastand and intratree spatial patterns of the western spruce budworm. For those sampling populations of the Douglas-fir tussock moth, Orgyia pseudotsugata (McD.), Mason (1978) noted that sampling variances associated with treated populations can be different from those in untreated ones.

After moth flight, redistribution of egg masses by females may effectively eliminate any significant direct effects of treatment on the sampling attributes of the budworm population. Before moth flight, however, spatial patterns of the population may be changed significantly by treatment. Until this question is resolved, managers should be particularly cautious in evaluating either the statistical precision or the biological meaning of post-treatment samples of larvae and pupae. For example, in the application of Abbott's formula (Abbott 1975) to evaluate the effects of a pesticide, pre-treatment and post-treatment samples taken from the same tree strata are assumed to bear the same relation to the target population. This implicit assumption should be tested.

Sequential Count Plans

Aerial sketch-mapping is commonly used to delineate an outbreak of the western spruce budworm. After the aerial survey is complete, more precise data on budworm density are often obtained from foliage samples taken from the midcrown

of normally sampled trees. Traditionally, the egg-mass sample has probably been the most routinely used, although larval sampling has also been common. Estimates of budworm densities derived from this work are used in both pre-treatment survey and post-treatment evaluation (Twardus 1985).

To use one of the count plans, a precision is fixed and the appropriate table selected. For example, Table 4 would be used to obtain an estimate of nominal fourth-instar density on sample tips of normally sampled trees. In each small (about 5-ha) block, 7- to 14-m-tall trees should be randomly selected, and one 45-cm terminal branch tip should be drawn from the midcrown of each tree.

Sampling continues until the total number of larvae equals or exceeds the number specified in the appropriate column. Thus, to obtain a larval estimate with a 20-percent precision, sampling would continue if less than 79 budworm larvae had been found on the first 20 tips. Sampling would stop, however, if at least 67 larvae had been found on the first 25 tips. For normally sampled trees, comparable "stop sampling" values for 25 sample tips for residual pupae (Table 7) and egg masses (Table 9) are 59 pupae and 96 egg masses, respectively.

Estimating Average Whole-Plot Densities

Accurate estimates of stage-specific survival are crucial for the successful conduct of studies on pest population dynamics. For the western spruce budworm, the ~~logical~~ traditional basis for these estimates is successive estimates of

average budworm density per square meter of foliage across the whole plot. The bases for these whole-plot estimates are density relations among vertical thirds of the host trees in each height class (Campbell et al. 1984a), and estimates of the proportion of the total host foliage in each of these vertical strata.

Where intracrown patterns of budworm density are consistent, such as those described in Campbell et al. (1984a), and intracrown foliage relations are consistent, such as those described in Srivastava et al. (1984), average whole-plot density per square meter of foliage can be estimated from densities per square meter of foliage on tips drawn from representative crown strata. For example, for the conditions they studied in the Pacific Northwest,

Srivastava et al. (1984) showed that the average whole-plot density of nominal fourth instars and egg masses per square meter of foliage on normally sampled trees (WS_L and WS_E, respectively) can be estimated from larval or egg-mass density per square meter of foliage on midcrown 45-cm tips (X_L and X_E) as:

$$WS_L = 0.238\ X_L,\ (R^2 = 98\%,\ n = 21);$$

$$WS_E = 0.82\ X_E,\ (R^2 = 88\%,\ n = 50).$$

Clearly, accurate estimates of both intrastand patterns of budworm occurrence and the intrastand distribution of host foliage are critical to the conduct of studies on budworm population dynamics.

Patterns of Budworm Occurrence--Recent analyses of patterns of occurrence in western spruce budworm populations revealed that mean densities per square

meter of foliage on 45-cm terminal tips of branches from the midcrown of normally sampled trees could be used to approximate mean densities per square meter of foliage in most of the crown strata (trees in various height classes, vertical thirds among trees in a given height class, and portions of a branch) (Campbell et al. 1984a).

Unfortunately, validation of the patterns found by Campbell et al. (1984a) will be expensive and time-consuming. Until that validation is complete, prospective users can either assume that these patterns are valid for their particular conditions, or they can conduct traditional multicrown sampling. Users should not assume that the patterns described by Campbell et al. (1984a) are valid for their conditions if the populations under study are either more dense than those examined or outside the Pacific Northwest.

Area of a Sample Tip--The average foliage area of branch tips may vary, both among host species in an area and from one area to the next. Those who want to estimate whole-plot densities per unit of foliage should estimate average tip area directly from the measured length and width of each nominal 45-cm tip they sample.

Foliage Distribution--Estimates of within-tree foliage distribution used by Srivastava et al. (1984) were derived from felling and measuring foliage on 98 Douglas-fir and 41 grand fir. These 139 trees were all full-crown, open-grown specimens, about 9-m tall, from study plots in north-central Washington, eastern Oregon, central Idaho, and northwestern Montana. Among those trees,

the average proportion of foliage in each crown third was 23:36:41, from top to bottom.

The above proportion of foliage in each crown third (roughly 1:2:2, from top to bottom) is different from both the 1:3:1 ratio derived by Mason (1970), and the 1:3:5 ratio derived by Carolin and Coulter (1972). The 17 trees felled by Mason were 6 to 12 m tall, and the 15 used by Carolin and Coulter ranged from 16 to 24 m. Comparison among these three sets of ratios and tree heights suggests that within-tree foliage distribution may vary systematically as a function of tree height. Among short trees, a higher proportion of the foliage may be found in the midcrown. Among tall ones, more of the foliage may be in the lower crown. Users of these plans should select or derive estimates of within-tree foliage distribution appropriate to the conditions from which their samples are to be taken.

Classifying Expected Defoliation

Projecting Defoliation--Suppose the objective of the sampling is to use egg masses to classify expected defoliation as either light or moderate-to-heavy (Table 11A). Expected defoliation could be classified as moderate-to-heavy and sampling would stop if more than 5 egg masses had been found on the first five 45-cm tips drawn (one per tree) from the midcrowns of normally sampled trees. Expected defoliation could not be classified as light until no egg masses had been found on the first 15 tips sampled.

The sequential classification schemes were developed where categorizing the pest in terms of expected defoliation. Thus, the usefulness of these schemes is based in part on a satisfactory ability to project defoliation as a function of current pest density.

Recent experience with the western spruce budworm across four northwestern states has validated Carolin and Coulter's (1972) formula that relates defoliation at the end of a season to preceding fourth instar density. But defoliation in this four-state area was not well-correlated with preceding egg-mass density. To minimize the likelihood of error, provisional classification of expected defoliation based on the density of egg masses should be validated by further classification, based on the density of nominal fourth instars. The results presented here also strongly suggest that managers will be well advised to calibrate whatever predictive equations they use for local conditions before the values these equations project became part of the basis for critical management decisions.

Error Rates--Recently, Nyrop and Simmons (1984) critically reviewed Iwao's (1975) sequential classification procedure. Briefly, Nyrop and Simmons showed that the actual error rates that arise from the use of Iwao's classification plan are larger than the nominal ones. Interested users should consult this critique.

Each of the plans presented here is based on budworm sampling distributions found in small (5-ha) blocks. Where the sampling objective is to classify expected defoliation in a larger area, such as a third-order watershed,

managers should use the schemes provided (Tables 6 and 12) to classify defoliation in a series of subunits. If the classification of the larger area is based on results from several subunits, the danger of misclassifying the larger area should be very small.

Projecting Damage

Larvae of the western spruce budworm subsist primarily on current-year foliage. Even during severe outbreaks, only a small proportion of the older needles are eaten during any given season. As a consequence of this defoliation, increased photosynthetic activity of previously shaded older needles serves to buffer the effects of defoliation on the host trees. Thus, the likely consequences of one season of defoliation by this pest are only predictable when viewed in context with other variables. Van Sickle (1985) summarizes current information about the effects of defoliation and bud kill by the western spruce budworm on seed production, radial and height growth, top-kill, tree defect, mortality, and host vigor of trees and stands.

IMPLICATIONS

Spatial Pattern

Presumably, each of the patterns exhibited by any species have evolved because they confer some survival advantage. For example, the spatial patterns exhibited by late instars and pupae of the western spruce budworm can be presumed to yield higher survival, on average, than would result from either a more regular or a more aggregated pattern.

Aggregated individuals, once located, become easier prey for any given mortality-causing factor than would individuals in an equally dense, but more regularly distributed population (Ivlev 1961, Griffiths and Holling 1969). Thus, except for mating, the mortality consequences of aggregation appear likely to work against survival. Nevertheless, except at the lowest densities studied, the populations described here were invariably more aggregated than random on the branch tips of every crown stratum and at each of the three budworm stages.

Because predators commonly exhibit effective behavioral responses to a patchy or mosaic pattern of prey occurrence (Emlen 1973), one result of predation would reasonably be expected to be a reduction in the patchiness of the residual population of prey. Surprisingly, results described both here and elsewhere (Campbell et al. 1985) suggest that predation on late instars and pupae of the western spruce budworm tends to increase the residual patchiness of this prey species. In particular, both the extreme patchiness of residual

budworm pupae on lower crown tips, and the poor $m^* - m$ relation in this crown stratum suggest that the effectiveness of predaceous ants against the western spruce budworm tends to be highly variable literally from one tree to the next.

Clearly, patchy distributions are so common among organisms representing virtually all major taxa that their presence is usually taken for granted. Perhaps some degree of patchiness in the spatial pattern of a prey/host organism serves more to reduce the probability of random encounters with natural enemies than it does to risk the loss of several members when one of the "patches" is found.

The results presented here suggest that the degree of patchiness in the occurrence of residual pupae on lower crown tips could provide a useful index for evaluating patchiness in the suitability of any given habitat for predaceous ants.

Sequential Count Plans

With traditional, fixed-size sampling schemes, the sample size which must be specified in advance--must be large enough to provide acceptable precision wherever the scheme is to be applied. Under these schemes, sampling in some sites will necessarily continue after acceptable precision has been attained. For example, for any given budworm stage, a sample size sufficient to attain acceptable precision in sparse populations would result in considerable oversampling in dense ones. With sequential count plans, sampling at each site stops as soon as the prespecified precision has been reached. Thus, sequential

count plans should allow researchers and managers to estimate density at a prespecified precision at a lower average cost than would be needed for traditional fixed-size sampling schemes.

Estimating Average Whole-Plot Density

Accurate estimates of average whole-plot density are crucial for the successful conduct of studies on budworm population dynamics, but the cost of extensive multicrown sampling to derive these estimates has usually been beyond the means of prospective investigators. Now, in places where intrastand patterns of budworm occurrence are similar to those described by Campbell et al. (1984a), investigators can derive reliable estimates of average whole-plot budworm density by following the plans presented here to sample branch tips from the specified crown strata until the desired precision is reached, and, by using locally derived estimates of intrastand foliage distribution, weight the contribution of each crown third and tree height class.

To the extent that the above procedures reduce the need for multicrown sampling to estimate average whole-plot budworm density, they reduce the cost of conducting studies on budworm population dynamics.

Classifying Expected Defoliation

Together, the sequential classification scheme that uses egg masses and the one that uses fourth instars appear to provide a reasonable basis for classifying areas in terms of expected defoliation. For provisional decisions, the scheme

based on egg masses should provide pest-management experts with a relatively inexpensive alternative to traditional sampling. For final classification before a treatment decision must be made, the scheme based on nominal fourth instars should provide a speedy and accurate projection of expected defoliation.

SUMMARY

1. A study on spatial patterns and sampling attributes of the western spruce budworm was conducted on data collected between 1979 and 1982 from several sites in Washington, Idaho, Oregon, and Montana. In Oregon, the populations studied represented an early phase of a major outbreak; those in Idaho and Montana were part of dynamically stable, low intensity outbreaks; and those in Washington were studied during outbreak decline.

2. During each budworm generation, sampling was done three times: when most of the insects were in fourth instar; when adult emergence was about 95 percent complete; and when egg-mass deposition was complete. At each stage, sample units consisted of 45-cm terminal branch tips drawn from host Douglas-fir and grand fir.

3. Spatial patterns of the budworm were estimated by Lloyd's (1967) mean crowding index ($\overset{*}{m}$), and analyzed by Iwao's (1968) regression technique. Subsequently, for each budworm stage, sequential count plans were calculated by Kuno's (1969) method.

4. A model that relates fourth instars per 100 buds to subsequent defoliation (Carolin and Coulter 1972) was simultaneously tested against data from the Pacific Northwest, southwestern Montana, and northern New Mexico. Subsequently, Iwao's (1975) procedure was used to develop sequential classification plans for egg masses and fourth instars.

5. Except at the lowest densities sampled, budworm populations at all stages were more aggregated than random. Sample means and variances were usually about equal as mean densities approached the minimums sampled--about 0.1 insect or egg mass per tip. On tips drawn from the midcrown of normally sampled trees, fourth instars were less aggregated than either residual pupae or egg masses. At each stage, a single insect or egg mass appeared to form the basic component of the population on midcrown terminals.

6. Comparison between my results and those derived by other workers suggests that late instars of C. occidentalis in the Pacific Northwest may be somewhat more aggregated than other, more easterly populations of C. occidentalis, as well as populations of C. fumiferana. For both budworm species, egg masses may be somewhat less aggregated on the tallest host trees.

7. According to estimated values of the negative binomial parameter k. residual pupae on lower crown tips were more aggregated than those drawn from the midcrown. Based on these results and the relevant literature, I attributed the increased aggregation of pupae on lower crown tips largely to the activities of predaceous ants. Also, mean crowding of residual pupae on lower crown tips was poorly described by mean density. This low correlation was ascribed primarily to patchiness in the species composition, distribution, and intensity of predation by ant colonies.

8. Sequential count plans were developed for all three budworm stages on midcrown tips of normally sampled trees. For each stage, critical stop values are described for each of several specified precisions. Similar count plans are presented for residual pupae on midcrown tips of short (4-7 m) trees, and for egg-masses on lower crown tips of tall ones.

9. When estimates of fourth instar or pupal densities on short trees are needed, separate samples should be drawn from the midcrown of these trees. Similarly, separate fourth-instar or egg-mass samples should be drawn from the lower crown of tall trees, in places where estimates of these densities on tall trees are needed.

10. For several reasons, the lower crown should not be selected as the preferred stratum for sampling residual pupae.

11. My results strongly suggest that Carolin and Coulter's (1972) regression equation accurately projects defoliation in the Pacific Northwest from preceding fourth-instar density. From any given larval density, however, my results also project much higher defoliation in areas east of the Continental Divide.

12. Two sequential plans are presented that use budworm densities on midcrown tips of normally sampled trees to classify expected defoliation. One plan uses egg masses. The second plan uses subsequent fourth instars.

13. For any given precision, optimal sample size varies inversely with population density. Alternative count plans should be used to estimate required sample sizes where densities are below about 0.1 insect or egg mass per tip.

14. To use any of these plans in large forested blocks, samples should be obtained from a representative series of approximately 5-ha subunits.

15. At least before moth flight, spatial patterns of the budworm may be changed significantly by pesticidal treatment. This possibility deserves investigation.

16. Until the patterns of budworm occurrence described by Campbell et al. (1984a) have been either validated or invalidated, prospective users can either assume that these patterns are valid for their conditions, or they can conduct traditional multicrown sampling.

17. Those who want to estimate whole-plot densities per unit of foliage should estimate average tip area directly. Such users should also select or derive appropriate estimates of intrastand foliage distribution.

18. Provisional classification of expected defoliation based on egg masses should be validated by further classification based on fourth instars.

19. Relations between budworm density and subsequent defoliation appear to vary systematically among geographic areas. Managers should calibrate whatever predictive equations they use for local conditons.

20. The likely consequences of one season of defoliation by the western spruce budworm are only predictable when viewed in context with other variables.

21. Some degree of patchiness in the occurrence of a species may serve more to reduce the probability of random encounters with natural enemies than it does to risk the loss of several members when a "patch" is found.

22. Sequential count plans should allow investigators to estimate density at a specific precision at a lower average cost than would be needed for fixed-size schemes.

23. In places where intrastand patterns of budworm occurrence are similar to those described in Campbell et al. (1984a), investigators can greatly reduce the cost that would be incurred by traditional multicrown sampling to derive estimates of average whole-plot density.

24. Together, the two sequential classification schemes appear to provide a reasonable basis for classifying expected defoliation.

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Table 1.--Samples for nominal fourth instars. All samples were 45-cm terminal branch tips drawn from the midcrowns of 7- to 14-m-tall trees.

Location	Year	Number of sites	Range in number of samples drawn per site	Range in mean number of larvae found per sample
Washington	1979	4	30 to 60	6.200 to 14.333
Washington	1980	4	64 to 68	1.441 to 10.797
Washington	1981	2	56 to 60	0.196 to 15.283
Idaho	1980	4	75 to 141	0.333 to 9.395
Idaho	1981	3	10 to 43	0.093 to 8.700
Montana	1981	4	46 to 56	0.018 to 12.915
Montana	1982	4	25 to 60	0.083 to 10.00
Oregon	1981	2	18 to 22	0.591 to 1.555
Oregon	1982	4	30 to 65	3.569 to 17.633
All	All	31	10 to 141	0.018 to 17.633

Table 2.--Samples for residual pupae. All samples were 45-cm terminal tips.

Location	Year	Number of sites	Range in number of samples drawn per site	Range in mean number of pupae found per sample
		Midcrown Samples from 7- to 14-m-tall trees		
Washington	1979	4	30 to 31	0.367 to 1.567
Washington	1980	4	128 to 151	.023 to 2.163
Washington	1981	1	40	0.600
Idaho	1980	4	75 to 138	.007 to 1.296
Idaho	1981	3	24 to 83	.012 to 1.833
Idaho	1982	5	26 to 52	.019 to 3.051
Montana	1981	9	40 to 54	.111 to 2.150
Oregon	1981	4	64 to 77	.039 to 2.406
Oregon	1982	5	20 to 39	.184 to 3.846
All	All	39	20 to 151	0.007 to 3.846
		Lower-crown Samples from 7- to 14-m-tall trees		
Washington	1980	2	32 to 37	.027 to 1.563
Washington	1981	1	60	.650
Idaho	1980	3	25 to 46	.600 to 1.444
Idaho	1981	2	25 to 59	.542 to 1.720
Idaho	1982	3	37 to 40	.775 to 1.270
Montana	1981	9	40 to 54	.129 to 1.675
Montana	1982	3	88 to 150	1.107 to 2.409
Oregon	1981	3	66 to 69	.136 to 1.478
Oregon	1982	9	20 to 200	.105 to 1.632
All	All	35	20 to 200	0.027 to 2.409
		Midcrown samples from 4- to 7-m-tall trees		
Idaho	1982	3	30 to 36	.500 to 2.033
Oregon	1982	5	12 to 38	.167 to 1.778
All	--	8	12 to 38	.167 to 2.033

Table 3.--Samples for egg masses. All samples were 45-cm terminal tips.

Location	Year	Number of sites	Range in number of samples drawn per site	Range in mean no. of egg masses found per sample
Midcrown samples from 7- to 14-m-tall trees				
Washington	1979	4	25 to 31	0.120 to 0.321
Washington	1980	4	36 to 49	.091 to 3.796
Washington	1981	1	36	.222
Idaho	1980	4	75 to 126	.028 to .508
Idaho	1981	2	28 to 46	.500 to 1.457
Montana	1981	9	36 to 52	.157 to 4.250
Montana	1982	3	51 to 52	.654 to 1.863
Oregon	1981	5	56 to 117	.113 to .941
Oregon	1982	4	46 to 63	.134 to .807
All	All	36	25 to 126	0.028 to 4.250
Lower crown samples from trees >14-m tall				
Montana	1981	4	14 to 18	0.056 to 3.111
Oregon	1981	5	10 to 74	.254 to 1.300
Oregon	1982	4	24 to 98	.204 to .917
All	All	13	10 to 98	0.056 to 3.111

Table 4.--Fourth-instar sample sizes required for normally sampled trees, to achieve various precisions relative to the mean, based on the standard error of the mean (65% confidence interval).

A. Cumulative number of larvae

Number of samples	Precision				
	10%	15%	20%	25%	30%
5	--	--	--	--	105
10	--	--	545	66	32
15	--	--	110	45	26
20	--	417	79	39	24
25	--	219	67	36	23
40	2,179	128	55	32	21
50	645	112	52	31	21
100	268	90	47	29	20
200	207	82	45	28	20
500	183	78	43	28	19
1000	176	77	43	28	19

B. Number of samples

Density per 45-cm tip	Precision				
	10%	15%	20%	25%	30%
0.1	1,725	767	432	276	192
0.25	713	317	179	114	80
0.5	375	167	94	60	42
1.0	206	92	52	33	23
2.5	105	47	27	17	12
5.0	71	32	18	12	8
10.0	54	24	14	9	6
15.0	49	22	13	8	6
20.0	46	21	12	8	6

Table 5.--Fourth-instar sample sizes required to achieve 20% precision relative to the mean, based on the standard error of the mean (65% confidence interval). C. occidentalis versus C. fumiferana. Data on C. fumiferana from Regniere and Sanders (1983).

Density per 45-cm tip	Number of samples	
	C. occidentalis	C. fumiferana
0.1	432	492
0.25	178	292
0.5	94	88
1.0	52	52
2.5	27	26
5.0	18	16
10.0	14	9

Table 6.--Means and negative binomial k's for residual pupae on 45-cm branch tips drawn from 7- to 14-m-tall trees.

State	Year	Site	Midcrown Mean	Midcrown k	Lower crown Mean	Lower crown k
Idaho	1980	330	1.073	1.03	1.239	0.58
Idaho	1980	350	1.296	3.43	1.444	2.00
Idaho	1980	360	0.307	0.75	0.600	0.49
Idaho	1981	330	0.883	1.09	0.542	1.29
Idaho	1981	350	1.833	1.88	1.720	0.81
Idaho	1982	320	1.550	3.18	0.775	0.32
Idaho	1982	321	3.051	1.84	1.270	1.27
Idaho	1982	330	1.475	1.28	1.200	2.38
Montana	1981	10	1.644	1.92	1.000	1.22
Montana	1981	30	0.111	-1.18/a	0.130	0.73
Montana	1981	40	2.200	25.20	0.889	1.49
Montana	1981	150	0.800	20.76	0.200	2.60
Montana	1981	160	0.625	3.05	0.550	2.65
Montana	1981	170	0.975	2.86	1.050	0.75
Montana	1981	180	1.225	3.85	0.675	0.87
Montana	1981	190	2.150	2.40	1.675	1.72
Montana	1981	200	1.775	2.34	1.075	0.70
Washington	1980	400	2.163	2.16	1.563	1.06
Washington	1980	450	0.033	-1.25	0.027	26.64
Washington	1981	400	0.600	1.71	0.650	0.85
Oregon	1981	111	1.348	0.45	0.928	1.13
Oregon	1981	121	2.406	2.02	1.478	0.75
Oregon	1981	210	0.219	0.42	0.136	0.42
Oregon	1982	121	3.846	1.31	1.632	1.44
Oregon	1982	130	1.588	0.63	1.118	2.96
Oregon	1982	210	1.650	1.66	0.850	0.84
Oregon	1982	250	0.184	-1.13	0.105	0.24
Oregon	1982	260	0.667	3.87	0.633	0.36

a Negative values of k indicate distributions that are more regular than random.

Table 7.--Pupal sample sizes required for normally sampled trees to achieve various precisions relative to the mean, based on the standard error of the mean (65% confidence interval).

A. Cumulative number of pupae and pupal cases

Number of samples	Precision 10%	15%	20%	25%	30%
5	--	--	--	--	--
10	--	--	--	186	31
15	--	--	518	41	20
20	--	--	88	30	17
25	--	--	59	26	15
40	--	122	39	21	14
50	--	91	35	20	13
100	234	60	30	18	12
200	140	51	27	17	12
500	113	47	26	17	12
1,000	107	46	26	17	12

B. Number of samples

Density per 45-cm tip	Precision 10%	15%	20%	25%	30%
0.1	1,058	470	265	170	118
0.25	458	204	115	74	51
0.5	258	115	65	42	29
1.0	158	70	40	26	18
2.5	98	44	25	16	11
5.0	78	35	20	13	9

Table 8.--Pupal sample sizes required for short trees to achieve various precisions relative to the mean, based on the standard error of the mean (65% confidence interval).

A. Cumulative number of pupae and pupal cases

Number of samples	Precision 10%	15%	20%	25%	30%
5	--	--	--	--	--
10	--	--	--	--	106
15	--	--	--	114	28
20	--	--	--	45	21
25	--	--	129	33	18
40	--	422	51	24	15
50	--	157	42	22	14
100	513	70	32	19	13
200	168	55	28	18	12
500	120	48	27	17	12
1,000	109	47	26	17	12

B. Number of samples

Density per 45-cm tip	Precision 10%	15%	20%	25%	30%
0.1	1,081	481	271	173	121
0.25	481	214	121	77	54
0.5	281	125	71	45	32
1.0	181	81	46	29	21
2.5	121	54	31	20	14

Table 9.--Egg-mass sample sizes required from midcrowns of normally sampled trees, to achieve various precisions relative to the mean, based on the standard error of the mean (65% confidence interval).

A. Cumulative number of egg masses

Number of samples	Precision				
	10%	15%	20%	25%	30%
5	--	--	--	--	--
10	--	--	--	--	55
15	--	--	--	71	28
20	--	--	190	44	23
25	--	--	96	36	21
40	--	218	55	28	18
50	--	139	48	26	17
100	381	81	39	23	16
200	191	67	35	22	15
500	147	61	33	21	15
1,000	137	59	33	21	15

B. Number of samples

Density per 45-cm tip	Precision				
	10%	15%	20%	25%	30%
0.1	1,338	595	335	214	149
0.25	575	256	144	92	64
0.5	321	143	81	52	36
1.0	194	87	49	31	22
2.5	118	53	30	19	14
5.0	93	41	24	15	11

Table 10.--Egg-mass sample sizes required from lower crowns of tall trees to achieve various precisions relative to the mean, based on the standard error of the mean (65% confidence interval).

A. Cumulative number of egg masses

Number of samples	Precision 10%	15%	20%	25%	30%
5	--	--	--	--	58
10	--	--	195	48	25
15	--	2,032	79	35	21
20	--	232	61	31	20
25	--	151	53	29	19
40	780	100	45	27	18
50	411	90	43	26	18
100	212	74	39	25	17
200	170	69	38	24	17
500	153	66	37	23	16
1,000	147	65	36	23	16

B. Number of samples

Density per 45-cm tip	Precision 10%	15%	20%	25%	30%
0.1	1,455	647	364	233	162
0.25	602	268	151	97	67
0.5	318	141	80	51	36
1.0	175	78	44	28	20
2.5	90	40	23	15	10
5.0	62	28	16	10	7

Table 11.--Egg-mass classification scheme for categorizing populations at 95-percent confidence level.

A. Light versus moderate-to-heavy

Number of samples	Cumulative number of egg masses	
	Light	Moderate-to-heavy
5	<--	> 5
10	<--	> 9
15	< 1	>11
20	< 2	>14
25	< 3	>17
100	<25	>55

B. Light-to-moderate versus heavy

Number of samples	Cumulative number of egg masses	
	Light-to-moderate	heavy
5	<--	> 11
10	< 2	> 18
15	< 5	> 25
20	< 8	> 32
25	<12	> 38
100	<73	>127

Table 12.--Fourth-instar classification scheme for categorizing populations at 95-percent confidence level.

A. Light versus moderate-to-heavy

Number of samples	Cumulative number of larvae	
	Light	Moderate-to-heavy
5	< 3	> 27
10	<13	> 47
15	<24	> 66
20	<35	> 85
25	<47	>103
100	<244	>356

B. Light-to-moderate versus heavy

Number of samples	Cumulative number of larvae	
	Light-to-moderate	Heavy
5	< 14	> 66
10	< 43	>117
15	< 74	>166
20	<107	>213
25	<141	>259
100	<681	>919

FIGURE CAPTIONS

Figure 1.--Relation between mean fourth-instar density on midcrown 45-cm terminal tips of 7- to 14-m-tall trees and mean crowding. Solid line is regression ($\overset{*}{m} = 0.688 + 1.369\ m$). Dashed line is Poisson distribution.

Figure 2.--Fourth instars needed to obtain fixed precisions (D_o) on midcrown tips.

Figure 3.--Relation between mean density of residual pupae on midcrown 45-cm terminal tips of 7- to 14-m-tall trees and mean crowding. Solid line is regression ($\overset{*}{m} = 1.571\ m$). Dashed line is Poisson distribution.

Figure 4.--Relation between mean density of residual pupae on lower crown 45-cm terminal tips of 7- to 14-m-tall trees and mean crowding. Solid line is regression ($\overset{*}{m} = 0.474 + 1.646\ m$). Dashed line is Poisson distribution.

Figure 5.--Relation between mean density of residual pupae on midcrown 45-cm terminal tips of 4- to 7-m-tall trees and mean crowding. Solid line is regression ($\overset{*}{m} = 1.8049\ m$). Dashed line is Poisson distribution.

Figure 6.--Residual pupae needed from 7- to 14-m-tall trees to obtain fixed precisions (D_o) on midcrown tips.

Figure 7.--Residual pupae needed from 4- to 7-m-tall trees to obtain fixed precisions (D_o) on midcrown tips.

Figure 8.--Relation between mean egg-mass density on midcrown 45-cm terminal tips of 7- to 14-m-tall trees and mean crowding. Solid line is regression ($\overset{*}{m} = 0.271 + 1.666\ m$). Dashed line is Poisson distribution.

Figure 9.--Relation between mean egg-mass density on lower crown 45-cm terminal tips of trees > 14-m tall and mean crowding. Solid line is regression ($\hat{m} = 0.422 + 1.327\ m$). Dashed line is Poisson distribution.

Figure 10.--Egg masses needed from 7- to 14-m-tall trees to obtain fixed precisions (D_o) on midcrown tips.

Figure 11.--Egg masses needed from trees >14-m tall to obtain fixed precisions (D_o) on lower crown tips.

Figure 12.--Relation between fourth instars per 100 buds and subsequent percent defoliation. Data collected between 1979 and 1981 in the Pacific Northwest.

Figure 13.--Relation between fourth instars per 100 buds and subsequent percent defoliation. Data from southwest Montana.

Figure 14.--Relation between fourth instars per 100 buds and subsequent percent defoliation. Data from northern New Mexico.

Figure 15.--Comparative relations between fourth instars per 100 buds and subsequent defoliation. MT is southwest Montant; NM is northern New Mexico; GF is grand fir (Carolin and Coulter 1975); OR is eastern Oregon (Carolin and Coulter 1972); PNW is Pacific Northwest (1979-1981); and DF is Douglas-fir (Carolin and Coulter 1975).

Figure 16.--Chart to classify expected defoliation relative to two critical egg mass densities: (A) 0.4 egg masses per 45-cm tip; (B) 1.0 egg masses per 45-cm tip.

Figure 17.--Chart to classify expected defoliation relative to two critical fourth instar densities: (A) 3 fourth instars per 45-cm tip; (B) 8 fourth instars per 45-cm tip.

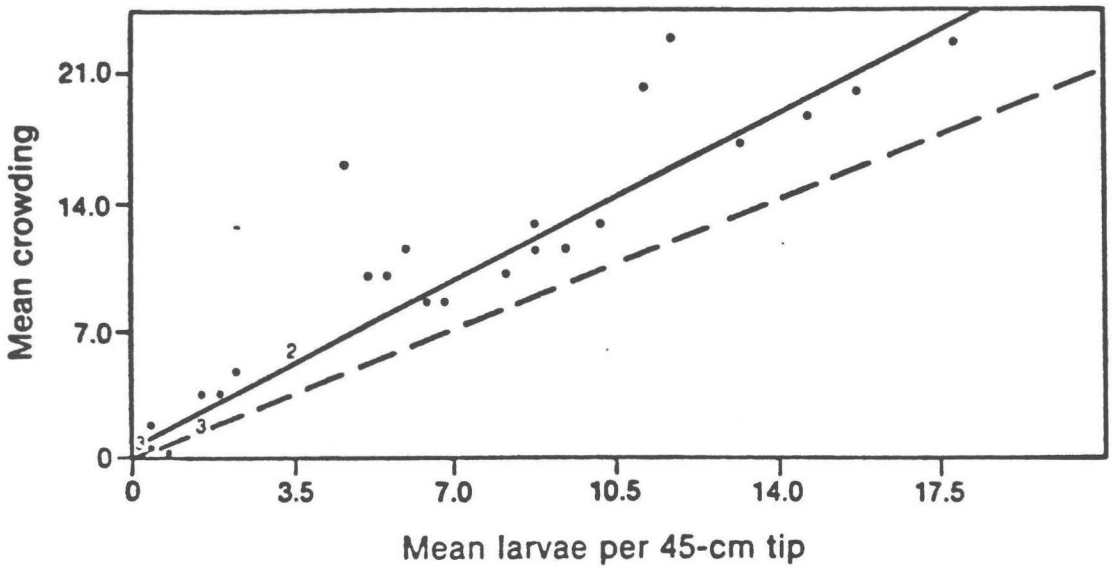


FIG. 1

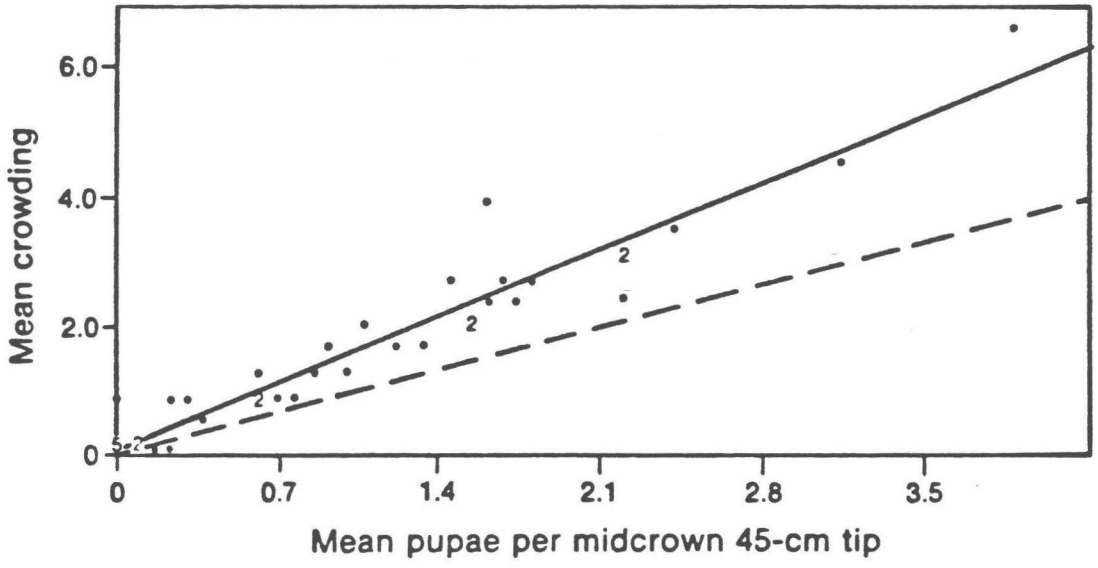


FIG. 3

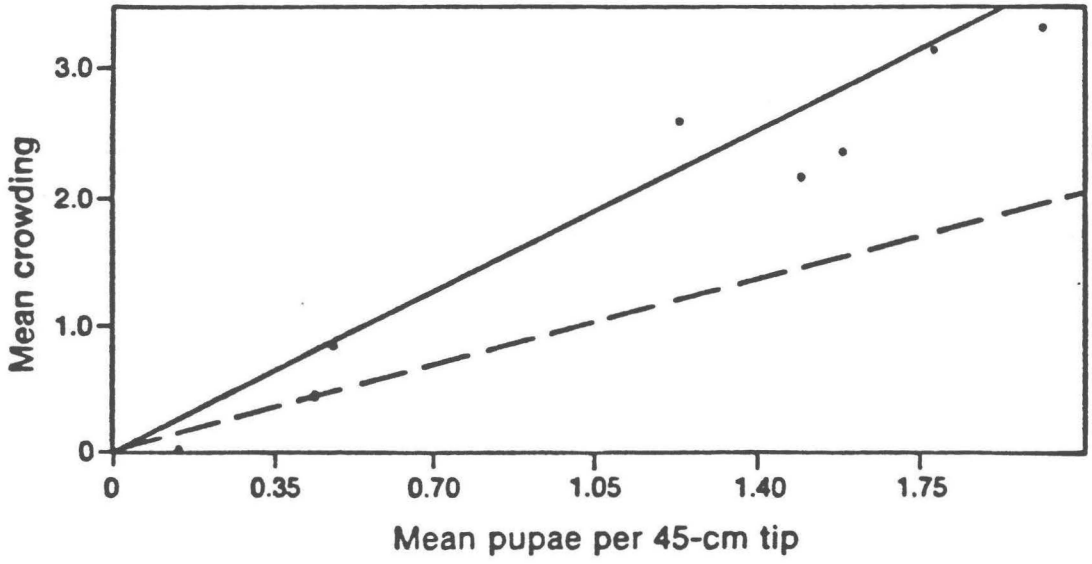
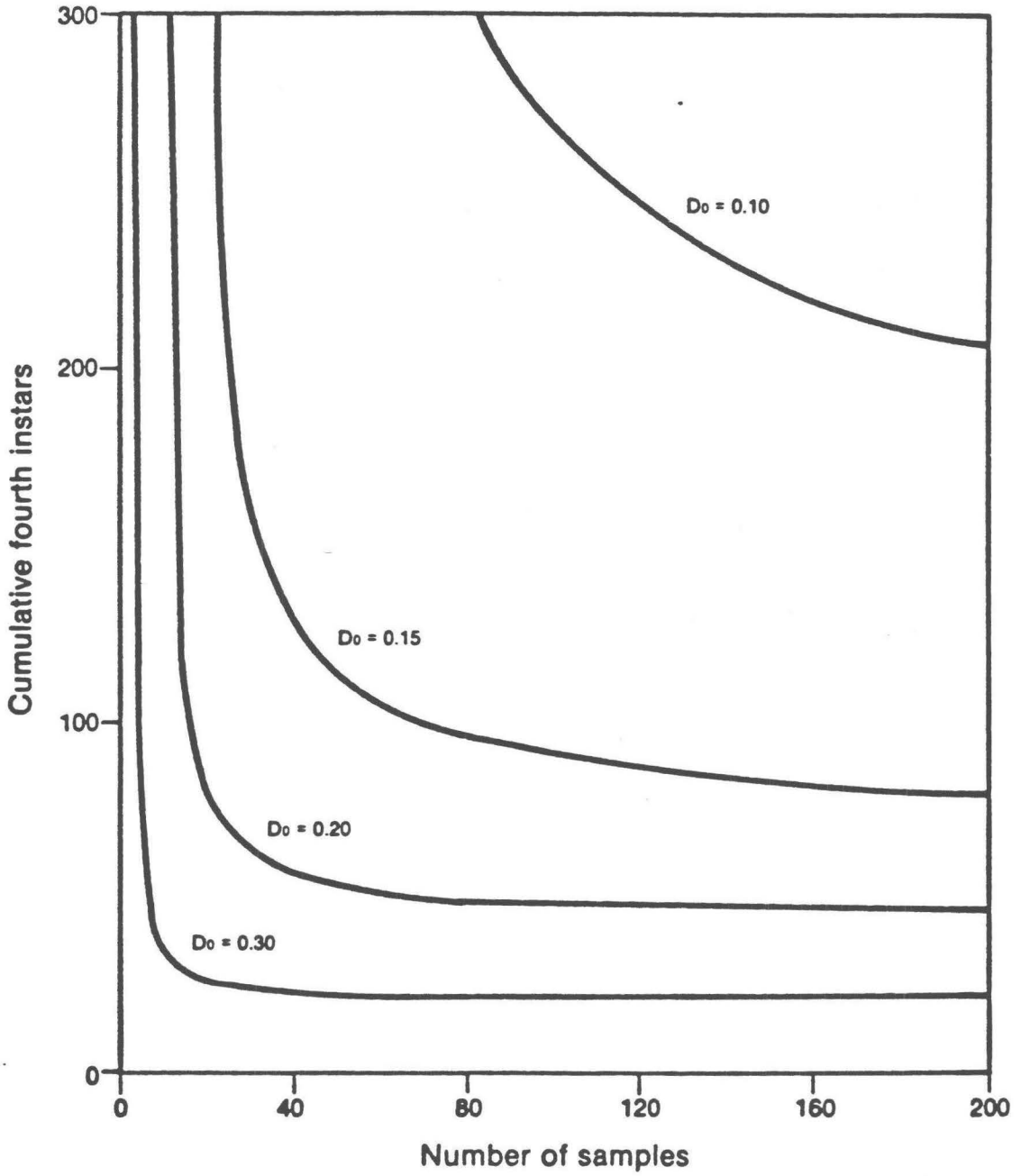


FIG. 5

FIG 2


300
200
100
0
Cumulative fourth instars
D0 = 0.10
D0 = 0.15
D0 = 0.20
D0 = 0.30
0
40
80
120
160
200
Number of samples

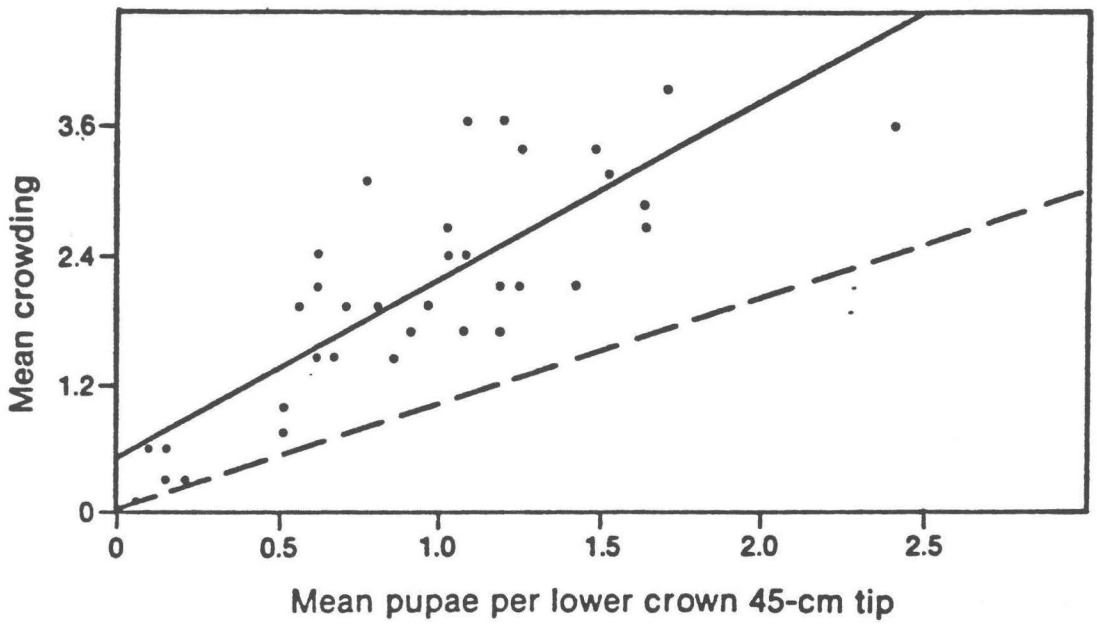

Mean crowding
3.6
2.4
1.2
0
0
0.5
1.0
1.5
2.0
2.5
Mean pupae per lower crown 45-cm tip

FIG 4

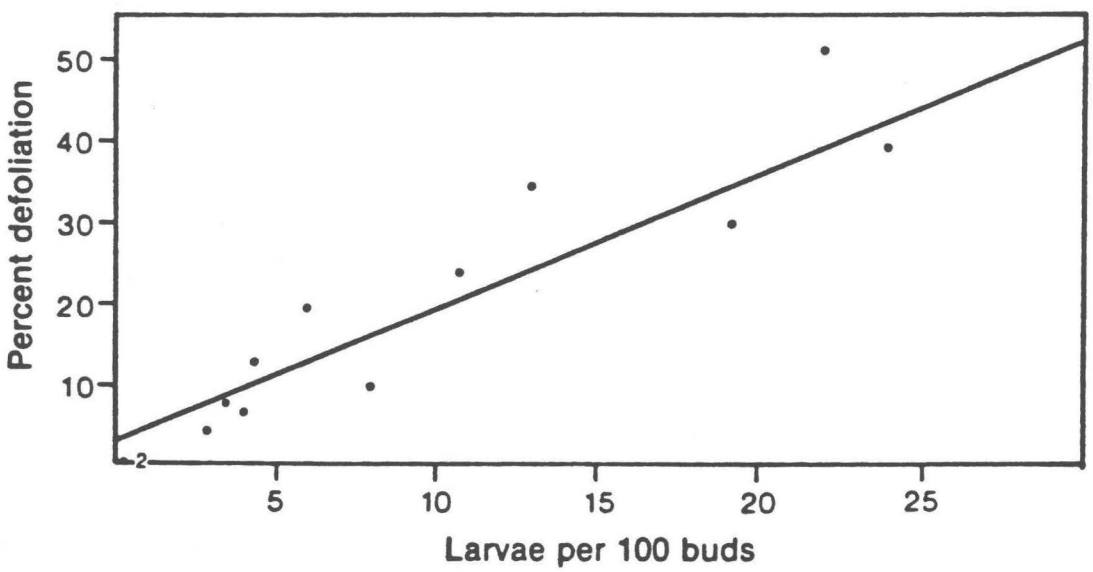

Percent defoliation
50
40
30
20
10
2
5
10
15
20
25
Larvae per 100 buds

FIG 12

FIG. 6

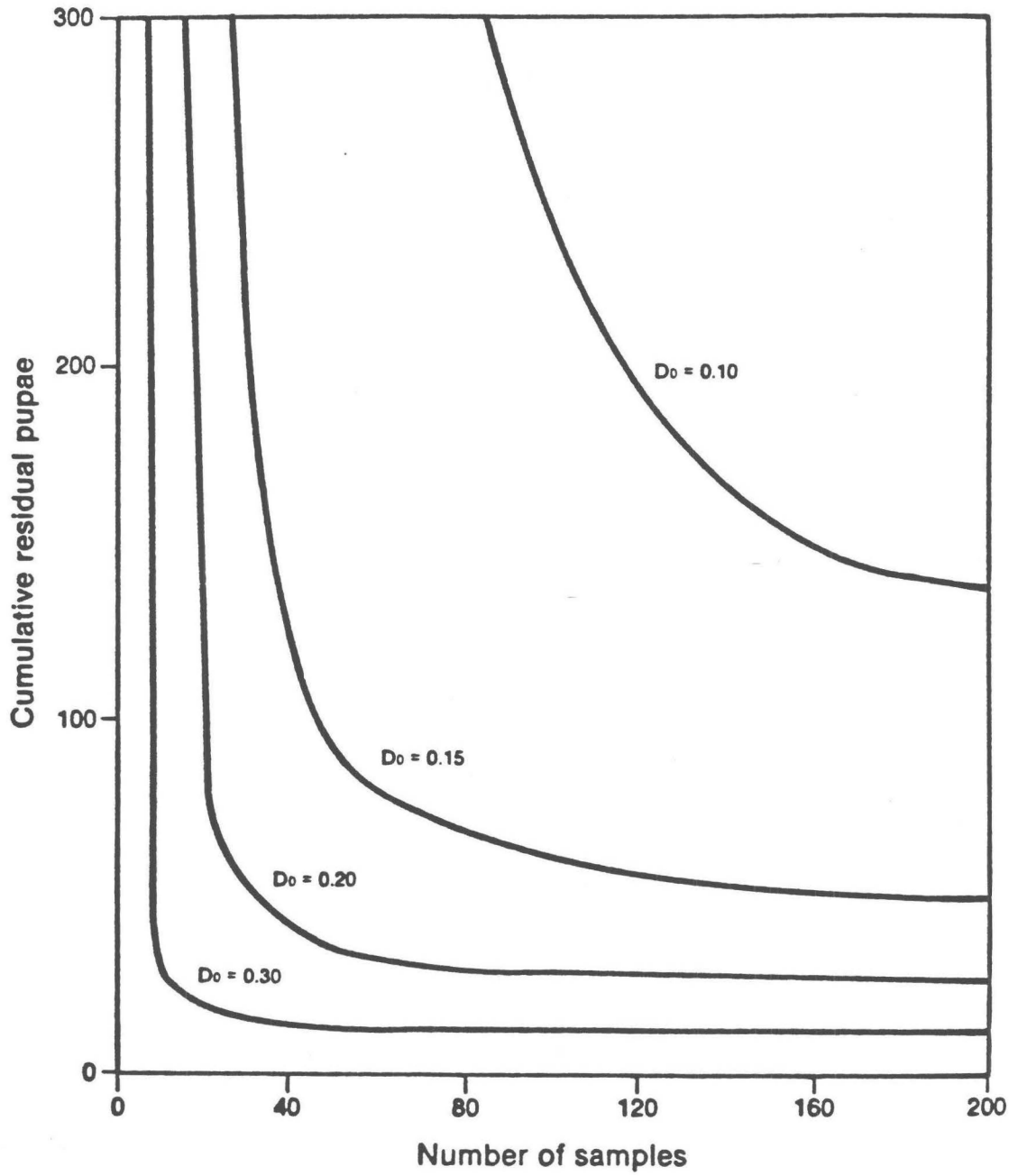
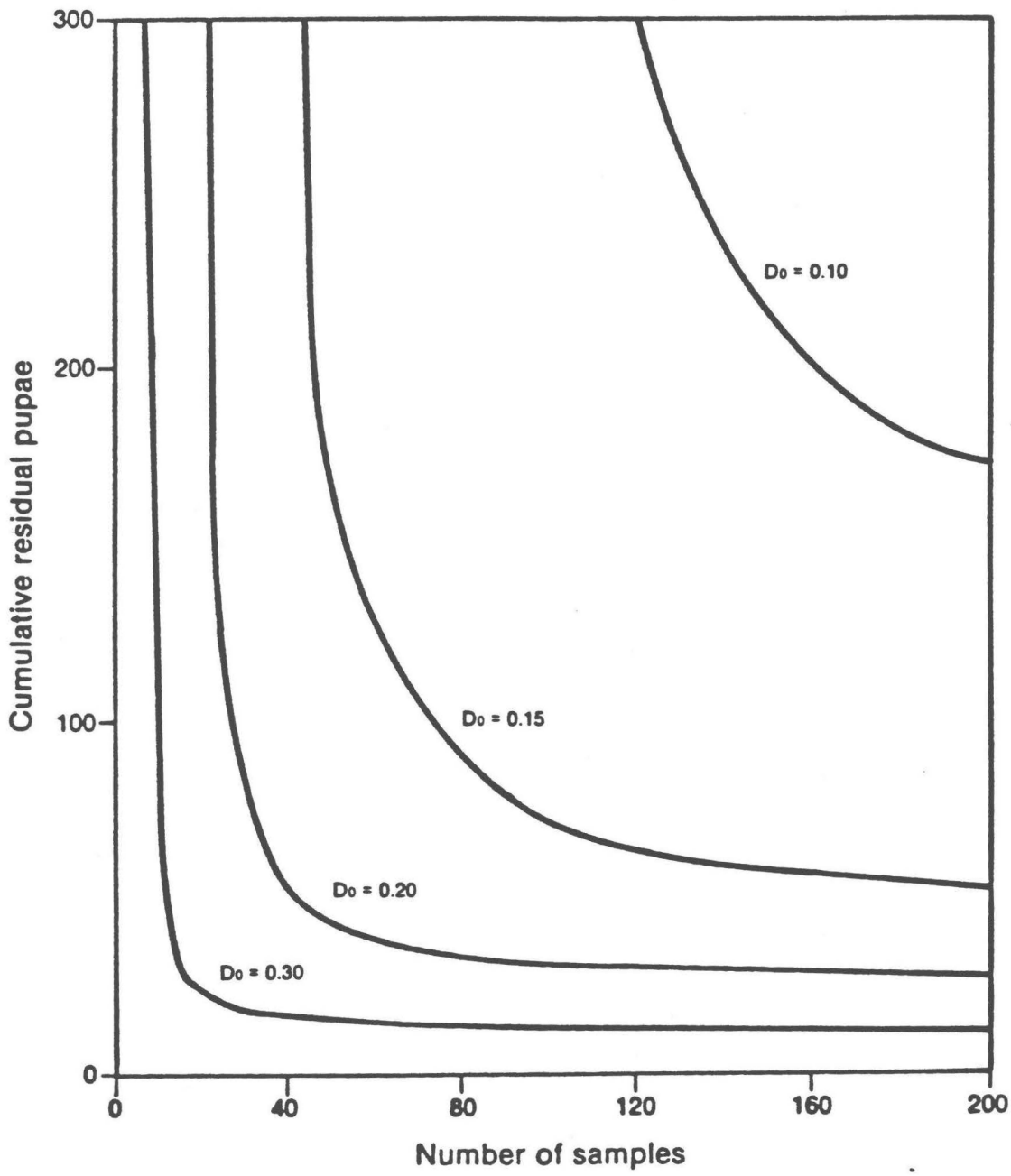

300
200
100
0
Cumulative residual pupae
D0 = 0.10
D0 = 0.15
D0 = 0.20
D0 = 0.30
0
40
80
120
160
200
Number of samples

FIG. 7


300
200
100
0
Cumulative residual pupae
D0 = 0.10
D0 = 0.15
D0 = 0.20
D0 = 0.30
0
40
80
120
160
200
Number of samples

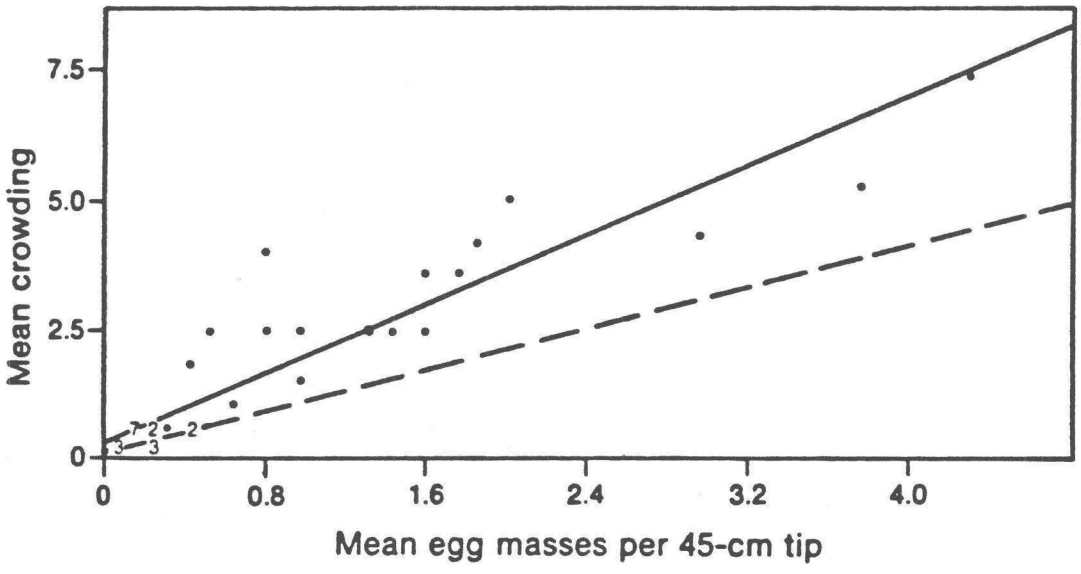

7.5
5.0
2.5
0
Mean crowding
0
0.8
1.6
2.4
3.2
4.0
Mean egg masses per 45-cm tip

FIG 7

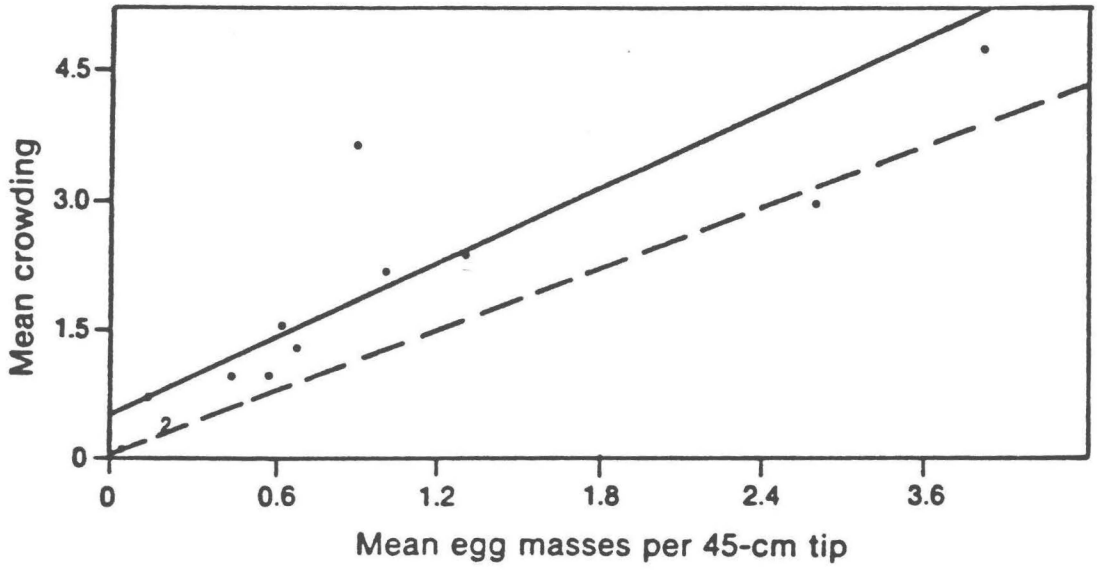

Mean crowding
4.5
3.0
1.5
0
0
0.6
1.2
1.8
2.4
3.6
Mean egg masses per 45-cm tip

FIG. 9

FIG 10

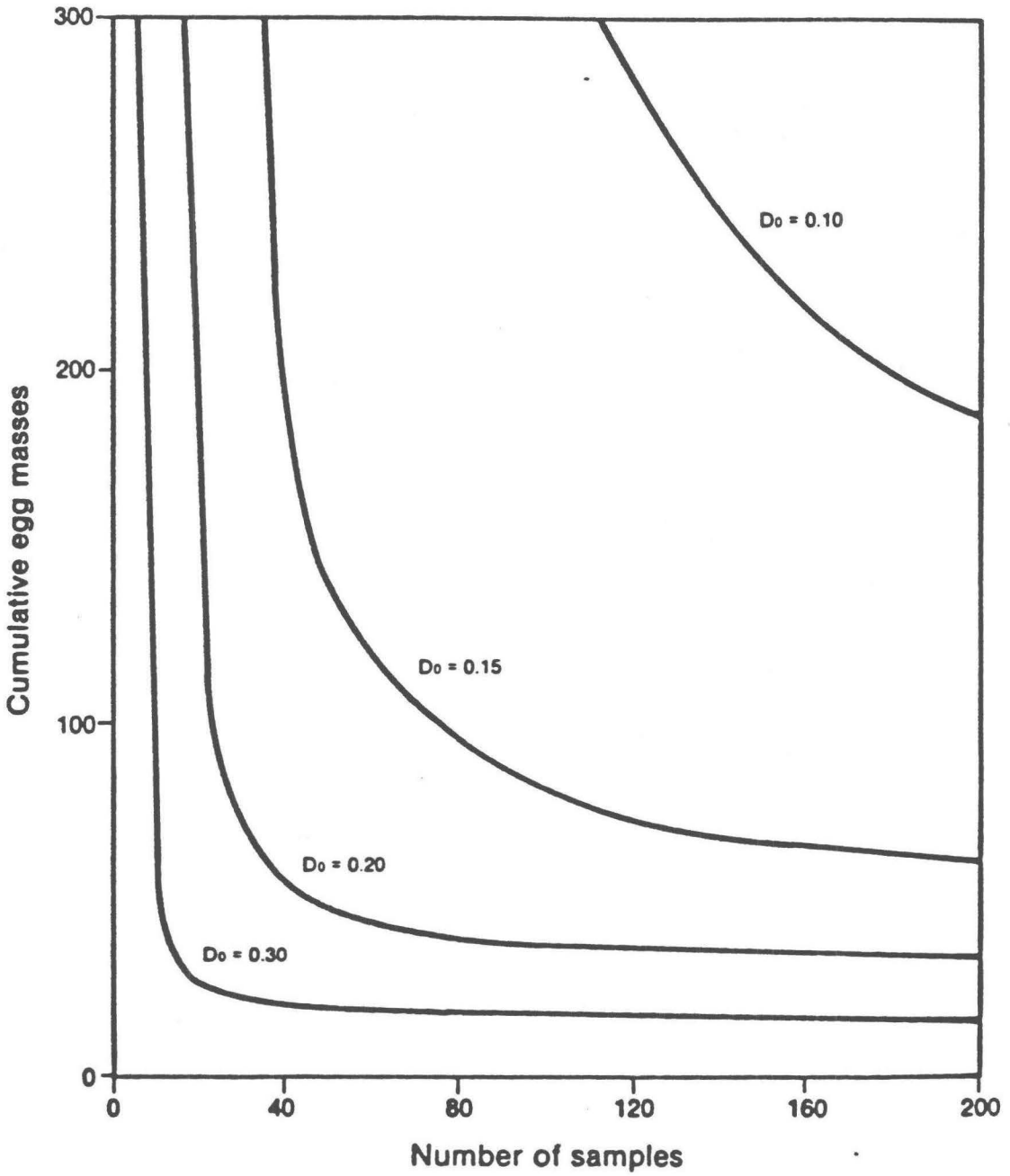
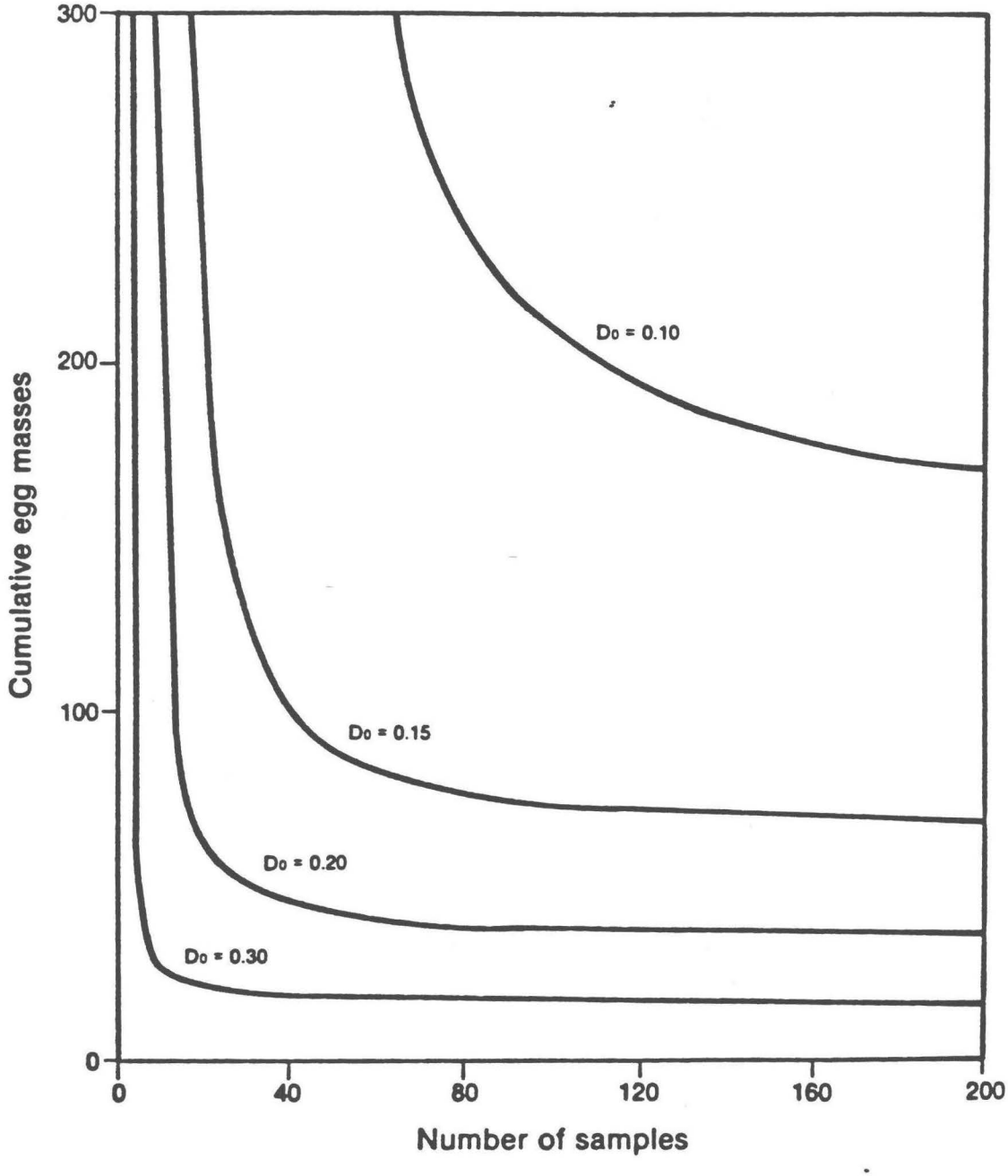

300
200
100
0
Cumulative egg masses
D0 = 0.10
D0 = 0.15
D0 = 0.20
D0 = 0.30
0
40
80
120
160
200
Number of samples

FIG 11


300
200
100
0
Cumulative egg masses
D0 = 0.10
D0 = 0.15
D0 = 0.20
D0 = 0.30
0
40
80
120
160
200
Number of samples

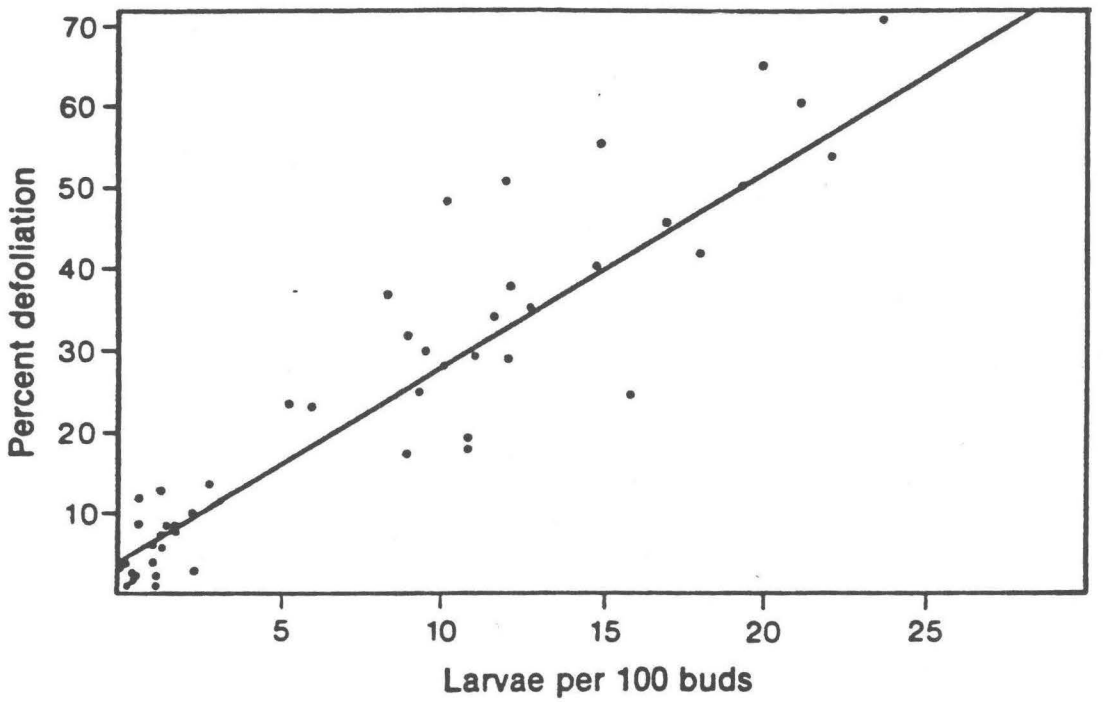

Percent defoliation
70
60
50
40
30
20
10
5
10
15
20
25
Larvae per 100 buds

FIG 1-1

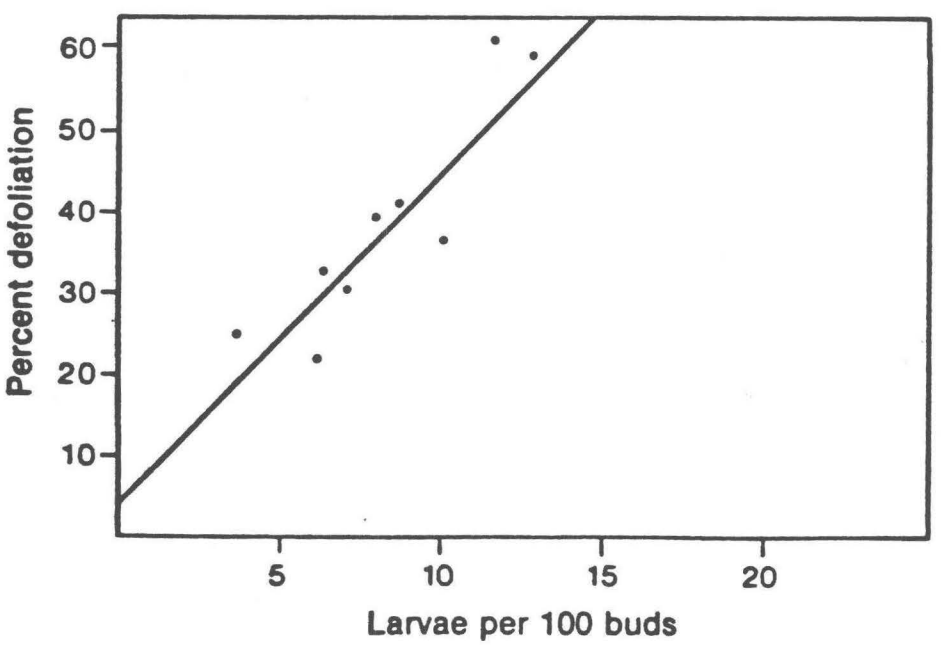

Percent defoliation
60
50
40
30
20
10
5
10
15
20
Larvae per 100 buds

FIG 13

F16 15

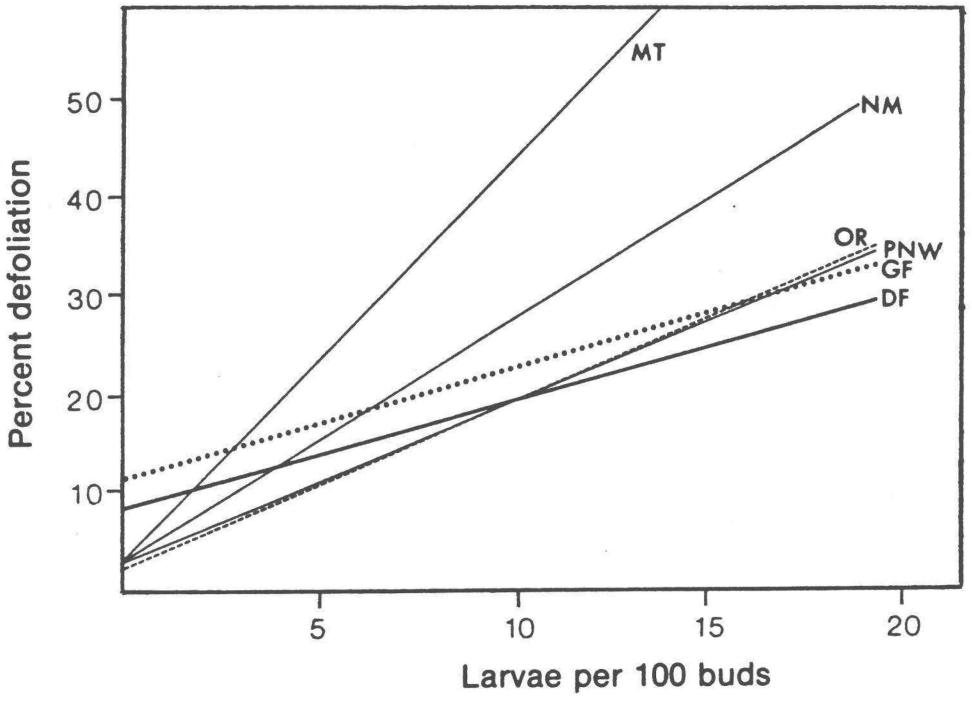
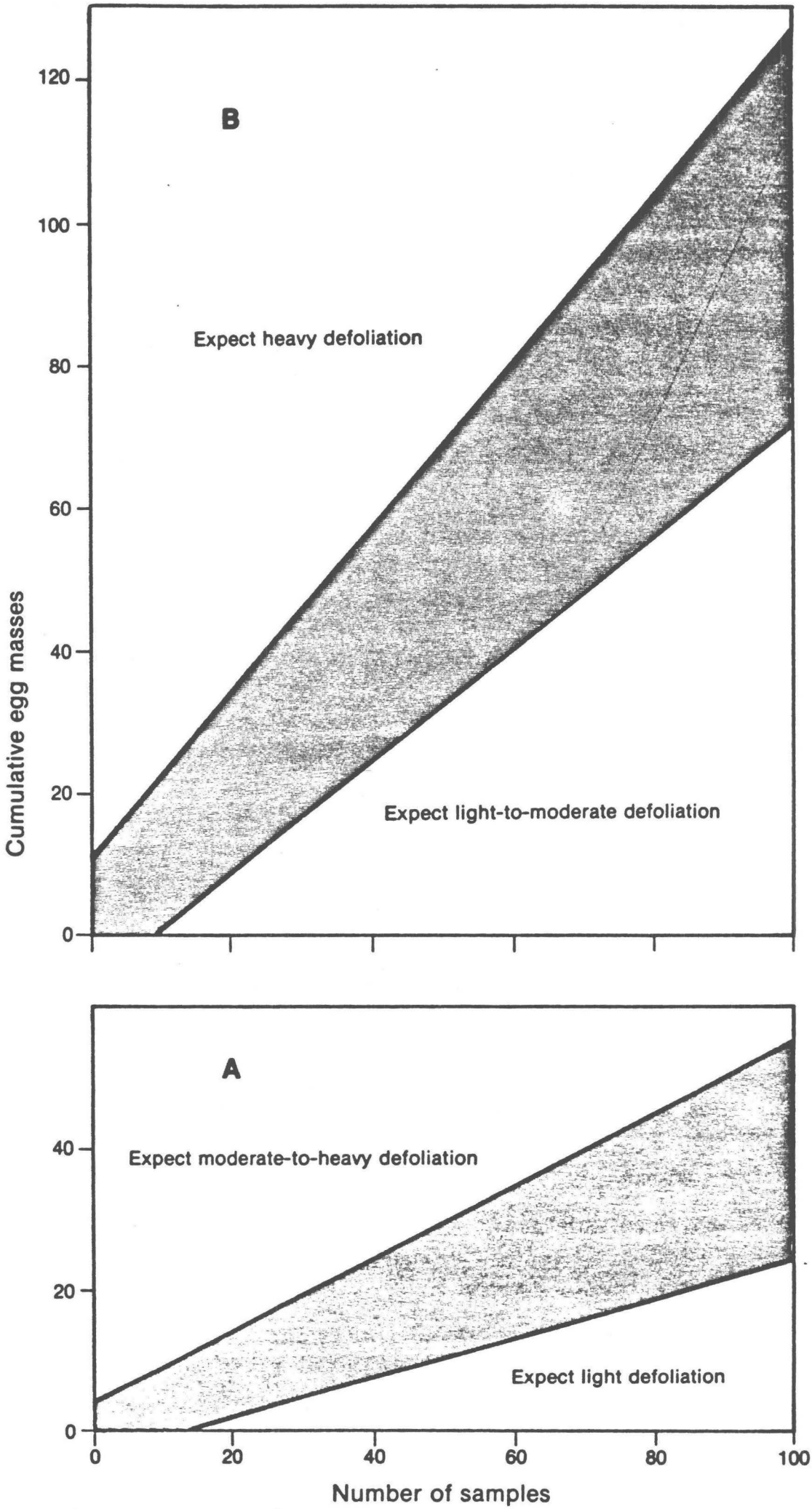
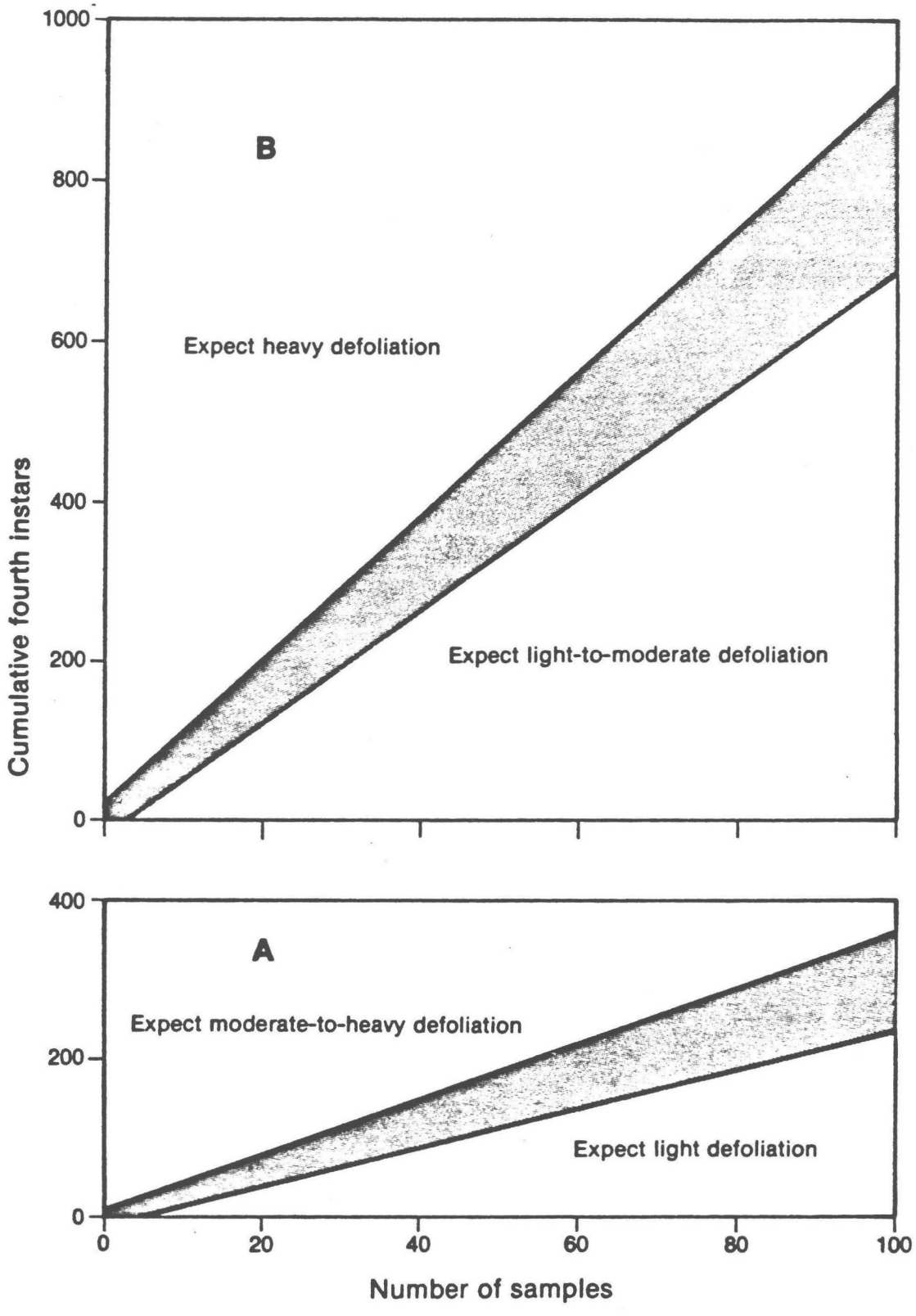

MT
NM
OR
PNW
GF
DF
50
40
30
20
10
Percent defoliation
5
10
15
20
Larvae per 100 buds

FIG 16


B
Expect heavy defoliation
Expect light-to-moderate defoliation
A
Expect moderate-to-heavy defoliation
Expect light defoliation
Cumulative egg masses
Number of samples
0
20
40
60
80
100
120


1000
800
600
400
200
0
B
Expect heavy defoliation
Expect light-to-moderate defoliation
Cumulative fourth instars
400
200
0
A
Expect moderate-to-heavy defoliation
Expect light defoliation
0
20
40
60
80
100
Number of samples